GRAZER RESPONSE TO FIRE IN AN AFRICAN SAVANNA:

EXPLORING THE ROLE OF FIRES IN GRAZING LAWN FORMATION.

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PREFACE

I, Adrian Drew Pollard (student number 770664), am a student registered for a Master of Environmental Science degree from 2013 to 2016 in the School of Animal, Plant, and Environmental Science at the University of the Witwatersrand. I hereby declare that this work is the product of my own independent research, unless otherwise acknowledged in the text, and it has not been submitted for any degree or examination at any other university. This dissertation was supervised by Sally Archibald (University of the Witwatersrand), with assistance from Catherine Parr (Liverpool University) and Navashni Govender (South African National Parks).

Adrian Drew Pollard

20th October 2016

Date

PLAGIARISM DECLARATION

I, Adrian Drew Pollard (student number 770664), am a student registered for a Masters degree from 2013 to 2016. I hereby declare the following:

1. I am aware that plagiarism (the use of someone else's work without their permission and/or without acknowledging the original source) is wrong.
2. I confirm that the work submitted for assessment for the above course is my own unaided work except where I have explicitly indicated otherwise.
3. I have followed the required conventions in referencing the thoughts and ideas of others.
4. I understand that the University of the Witwatersrand may take disciplinary action against me if there is a belief that this is not my own unaided work or that I have failed to acknowledge the source of the ideas or words in my writing.

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ABSTRACT

Fire and grazing are important drivers of grassland composition and function in savanna ecosystems. Fire alters the forage quality and vegetation structure, so changing fire regimes also changes grazer utilisation of the landscape. This study aimed to investigate how different fire regimes, specifically changes in fire size and season of burn, influence grazer attraction as well as grazing intensity and duration in the short-term, and further to determine how long-term fire-grazing interactions may influence the development of grazing lawns. In the short-term experiment, fires of three different sizes were applied in both the early dry season (EDS) and late dry season (LDS), and periodic collection of grass height and dung count data was conducted over a full year. Results showed that grazers were immediately attracted to the burned areas after the fires, and that fire and grazing together can maintain a short grazed patch for a full season. The greatest grazer visitation and grazing pressure (shortest grass) was observed on the intermediately sized burns (5ha). Furthermore, EDS treatments exhibited less initial grazer visitation but grass was kept in a short state for longer than on LDS burns. LDS burns had more intense grazing but over a much shorter time. For the long-term experiment, a long-standing fire experiment (Experimental Burn Plots, Kruger National Park, South Africa) was used to investigate change in grass community composition as influenced by fire-grazing interactions over a 60 year period. Historical data were used, and grass composition data were also collected on three treatments that allowed for comparison of communities that experienced grazing and fires repeated at different fire frequencies and different seasons (April biennial and August annual burns), as well as a natural fire regime (control). By investigating the change in abundance in a few key grass species, grass ecological status classes, and grass functional guilds, results found that grasses associated with grazing lawns (stoloniferous, ‘disturbed’) increased in abundance, while grasses of bunch grass communities decreased, and that this change was more pronounced on April biennial burns. The results of this study show that small fires can act as a catalyst for grass community compositional and structural change by attracting grazers.

Key words: Grazing lawns, fire size, fire season, pyric-herbivory, savanna.

DEDICATION

For my family.

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CHAPTER 1: INTRODUCTION

1.1. Introduction

Savannas are one of the largest biomes on the planet, constituting 20% of the earth's land surface. The dynamic co-dominance of both woody plants and grasses in African savanna ecosystems has resulted in substantial interest by scientists (Huntley and Walker, 1982; Belsky 1990), and much research suggests that fire, herbivory, climatic variability and soil fertility are the most significant drivers that interact and influence the dynamics of this relationship (Huntley & Walker, 1982; Scholes & Archer, 1997; Van Wilgen et. al., 2003). Fire and grazing are non-selective and selective consumers of vegetative biomass, respectively, and they both strongly influence system function through the alteration of the spatial heterogeneity of vegetation (Huntley & Walker, 1982; Milchunas & Lauenroth, 1993; Adler et al. 2001; Bond & Keeley, 2005; Yarnell et al., 2007), standing biomass (McNaughton, 1984;Bond & Keeley, 2005), both woody and herbaceous plant diversity (O'Connor, 1994; Jacobs & Naiman, 2008, Smith et al., 2012, Koerner et al., 2014), annual aboveground net primary productivity (Milchunas & Lauenroth, 1993), soil characteristics (McNaughton et al., 2001), and nutrient cycling (Hobbs et al., 1991; Van de Vijfer et al., 1999).

Fire is capable of influencing massive expanses of savanna vegetation, through the periodic removal of both grass and woody biomass, which is often followed by stimulated grass regrowth (Huntley and Walker, 1982; Scholes and Archer 1997; Bond et al. 2003). Although variable effects have been observed on savanna grasses with changes in fire regime (Everson & Tainton, 1984; Fynn et al., 2004, 2005), it is generally accepted that grass diversity composition is strongly influenced by fire frequency (Jacobs & Schloeder, 2002; Fynn et al., 2004) and that grass diversity decreases when fire is lacking (Fynn et al., 2005; Furley et al., 2008).It is understood that grass biomass (Van Wilgen et al., 2004), fuel moisture content and the weather conditions during burns (Higgins et al., 2000; Govender et al., 2006), all influence fire regimes (fire frequency, season of burn, fire intensity) in savanna systems.

The influence of grazing on vegetation is dependent on the existing spatial heterogeneity of vegetation, as well as on the patterns in which herbivores graze (Adler et al., 2001; Milchunas & Lauenroth, 1993; Yarnell et al., 2007). Grazing has the ability to stimulate grass regrowth that is of greater forage quality (improved nutrient content, McNaughton, 1983; Milchunas & Lauenroth, 1993; Adler et al., 2001; Fuhlendorf & Engle, 2004). It has been found that several biological factors influence mammalian grazer forage selection, and these include top-down (predator avoidance) and bottom-up (forage quality and quantity) processes (Sensenig et al., 2010; Luhdo, 2016), grazer feeding strategy (Sinclair et al., 2003), timing of reproduction and lambing (Main et al., 1996), and efficiency of foraging (Wilmshurst et al., 2000), and fires (Fuhlendorf & Engle, 2004; Archibald et al., 2005; Sensenig et al., 2010; Allred et al., 2011). Grazing is known to increase plant diversity in savannas, mainly by reducing competition (Collins et al., 1998), but this is dependent on climate, herbivore diversity, grazing intensity and system productivity (Milchunas et al., 1988; Olff & Ritchie, 1998; Bakker et al., 2006). Although high grazing pressure can cause loss of ground cover, soil erosion and overall ecosystem degradation (Tainton, 1972), it has been shown that grazing lawns can develop in areas of maintained heavy grazing (McNaughton, 1984; Archibald, 2008; Cromsigt & Olff, 2008; Bonnet et al., 2010; Hempson et al., 2014). Thus there are two very different ecological and grass community outcomes to heavy grazing, and it is not clear under which conditions each is likely to occur.

1.2. The fire-grazing interaction

The role of fire and grazing have been studied extensively, but very few researchers have considered the synergistic effect fire and grazing may have together on savanna systems (Archibald et al., 2005; Fuhlendorf et al., 2009). Fuhlendorf et al. (2009) suggest that all past research unnaturally decouples fire and herbivory as disturbance factors, and further proposes that the two disturbance factors be viewed as a single ecological interaction, in which each is spatially and temporally dependent on the other. Here, fire influences grazing by changing foraging patterns and in turn, herbivores influence fire by reducing fuel loads and the capacity of fire to spread in a landscape (Archibald et al., 2005). This interaction, ‘pyric-herbivory’, is described as “the spatial and temporal interaction between fire and grazing, where

positive and negative feedbacks promote a shifting pattern of disturbance across the landscape" (Fuhlendorf et al., 2009).

A conceptual model of the fire-grazing interaction (Figure 1.1) suggests that the interaction of fire and grazing takes place via positive and negative feedbacks which results in a changing vegetation matrix across the landscape (Fuhlendorf & Engel, 2004). This process creates new states and effects not observed if each process is investigated separately (Fuhlendorf & Engel, 2004; Archibald et al. 2005). In areas of higher biomass, accumulated over time in the absence of heavy grazing, the likelihood of fire is highest. Positive feedbacks occur when a fire attracts grazers to the newly burnt area, and negative feedbacks are observed when grass biomass is reduced through grazing. Grazing lowers the likelihood of a fire taking place, or decreases the intensity thereof, due to the reduction in available fuel. This in turn reduces the likelihood of grazing occurring on the burnt area. It is predicted that the dominance of tall grass species will decrease on newly burned areas, whereas the percentage of exposed ground and forbs will increase. This is expected due to the anticipated increased grazing intensity in newly burned areas, which is known to reduce tall grass species abundance and increase short grass species incidence. If areas are not burned, grazers are predicted to move into other areas of the landscape matrix, after which the tall grass species will recover. The result is a patchwork landscape of recently burnt and heavily grazed areas, found among areas in some form of a recovering state (Fuhlendorf & Engel, 2004). The effects of fire and grazing can interact and promote vegetative heterogeneity and diversity to a greater degree than if they were to act alone (Collins and Smith, 2006; Koerner and Collins, 2013). In this study, I propose that under certain conditions fire and grazing together can contribute towards grazing lawn development, an aspect of grazing lawn ecology that has not been studied before.

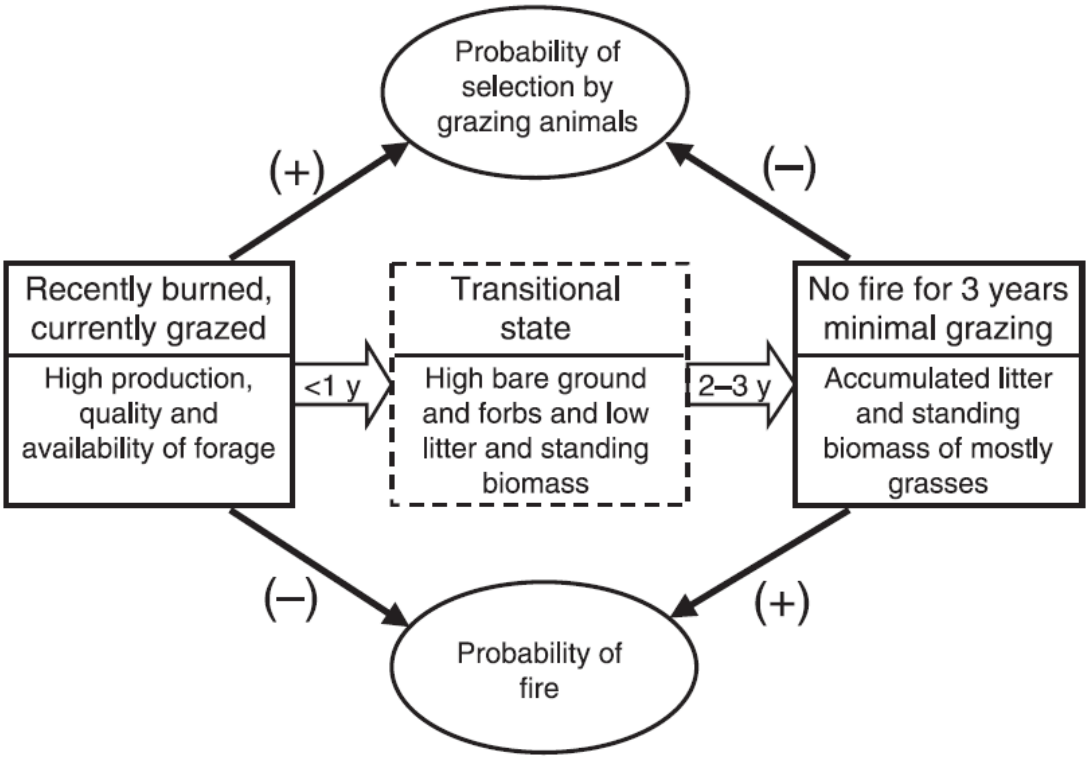

Figure 1.1 The fire-grazing interaction depicted in a conceptual model, exhibiting the dynamics of the changing vegetation matrix in a landscape. Each square represents a patch in the matrix that is experiencing a similar transitional state. The primary drivers of the interaction (fire and grazing) are represented by the Ovals, and solid arrows indicate the direction of the positive and negative feedbacks, influencing the likelihood of grazing selection or fire (Fuhlendorf & Engel, 2004).

1.3. Grazing lawns

As described in East Africa (Bell, 1970; McNaughton, 1984), West Africa (Verweijet al., 2006),and Southern Africa (Archibald et al., 2005; Waldram et al., 2007, Cromsigt & teBeest, 2014), grazing lawns are a widespread natural phenomenon in African savannas recognised as important landscape components that increase biodiversity at multiple trophic levels and play an important role in maintaining spatial heterogeneity (McNaughton, 1984; Novellie, 1990; Pickett, Cadenasso & Benning, 2003; Cromsigt & Olff, 2008). In his work investigating the effects of hippopotamus (*Hippopotamus amphibius*) grazing in the grasslands of western Uganda, Lock (1972) was the first to conceptualize the development of grazing grass communities that were dependant on grazing activity. However, the term “grazing lawn” was first popularized by McNaughton (1984) when he described it as a community of short

grass species that withstand and support heavy grazing, that provide large nutritional yield per bite. They are described as areas of short statured grasses, often members of the *Chorideae* family that can withstand frequent, intense defoliation and maintain a high leaf area index through horizontal growth. However their nature makes them susceptible to shading out by taller growth forms (McNaughton, 1984; Bond & Archibald, 2003; Hempson et. al., 2014). Such tufted or bunch grasses have an upright and caespitose appearance, and do not withstand greater grazing pressure (Bond & Archibald, 2003). Several interacting biological components contribute towards the development and maintenance of grazing lawns. These includes frequent grazing by both large (Cromsigt & teBeest, 2014) and smaller sized herbivores (Verwij et. al., 2006; Hempson et. al., 2014), as well as soil fertility, climatic variability, and fire (Archibald et. al., 2005; Masubele et al., 2007). Although herbivory is the key component for maintaining grazing lawns, they can be influenced by fire disturbance as well, through the influence that fire has on grazer attraction (Arsenault & Owen-Smith, 2008; Archibald, 2008; Allred et. al., 2011).

The creation of a shifting mosaic of tall grass areas and grazing lawns in savanna systems contribute significantly to system heterogeneity that promotes biological diversity of several trophic levels (Tilman & Downing, 1994; Fuhlendorf & Engle, 2001; Pickett et al., 2003; Cromsigt & Olff, 2008, Hempson et al., 2014). Therefore, it makes sense to aim to manage for a certain proportion of grazing lawns in many savanna and grassland environments (Novellie & Gaylard, 2013). There is no clarity in the literature about how much influence management has on grazing lawn extent – many grazing lawns are confined to locally enriched hot-spots such as old settlements, termite-mounds, or sodic sites (Young et al., 2005; Grant & Scholes, 2006; Fox et al., 2015), which implies that an external, abiotic driver is required to maintain the high levels of heavy grazing required for the formation of grazing lawns. However, it has also been shown that grazing lawn area and size are related to the levels of herbivory by the rhino mega-grazers (Cromsigt & teBeest 2014), which implies that their extent can be manipulated. Archibald (2008) and McNaughton (1984) suggested that positive feedbacks between short grass and grazing should be sufficient to initiate and maintain grazing lawns, but that external concentrating agents would help. In this regard, the way in which the fire-grazing interaction

influences grass communities and specifically how it may play a role in grazing lawn establishment has not been studied before.

1.3.1. Grazing lawn development and maintenance

Grazing lawns tend to develop where herbivory is frequent, and they are often associated with nutrient hot-spots (termite-mounds, old kraal sites) or water points (McNaughton, 1984; Grant & Scholes, 2006). Although these external factors help to maintain heavy grazing, McNaughton (1984) suggested that grazing lawns can develop in a homogeneous landscape through positive feedbacks with nutrients, and Archibald et al. (2005) demonstrated that short-grass alone is sufficient to attract grazers, and create positive feedbacks with grazing. In a recent review, Hempson et al. (2014) examined the factors influencing the dynamics of grazing lawns, and broadly investigated the role grazing lawns play in ecosystems. Through this they developed a conceptual model to describe the potential theoretical distribution and establishment of grazing lawns (Figure 3.1). They further show clearly how rainfall, soil nutrient status, mega-herbivore presence, the occurrence of facultative grass species, and predation risk play an important role in the establishment of grazing lawns and their distribution:

Rainfall, most importantly, influences the rate of biomass accumulation as well as the height to which grass grows. Therefore, Hempson et al. (2014) argue that in areas of greater rainfall (where grass regrowth rates are high), which also has high grazing pressure, translates to a reduction in the time needed to establish a grazing lawn. The importance of elevated soil nutrient patches (e.g. nutrient hotspots or sodic sites, Archibald, 2008) due to their ability to encourage frequent grazing pressure on short grass areas is emphasized. Hempson et al. (2014) suggest that nutrient rich areas in higher rainfall regions may be important for lawn establishment, specifically after fire disturbances, due to the dispersing effect that new grass regrowth has on grazers at this time (Archibald, 2005). Megaherbivores, particularly white rhinoceros (Cromsigt & teBeest, 2014) and hippopotamus (Lock, 1972), play a significant role in the establishment and maintenance of grazing lawns, especially in tall grass areas, due to their ability to consume large amounts of biomass. The pre-existence of facultative lawn grass species in tall grass systems improves the likelihood of lawn establishment. They are in fact likely to persist in such systems during lulls in grazing

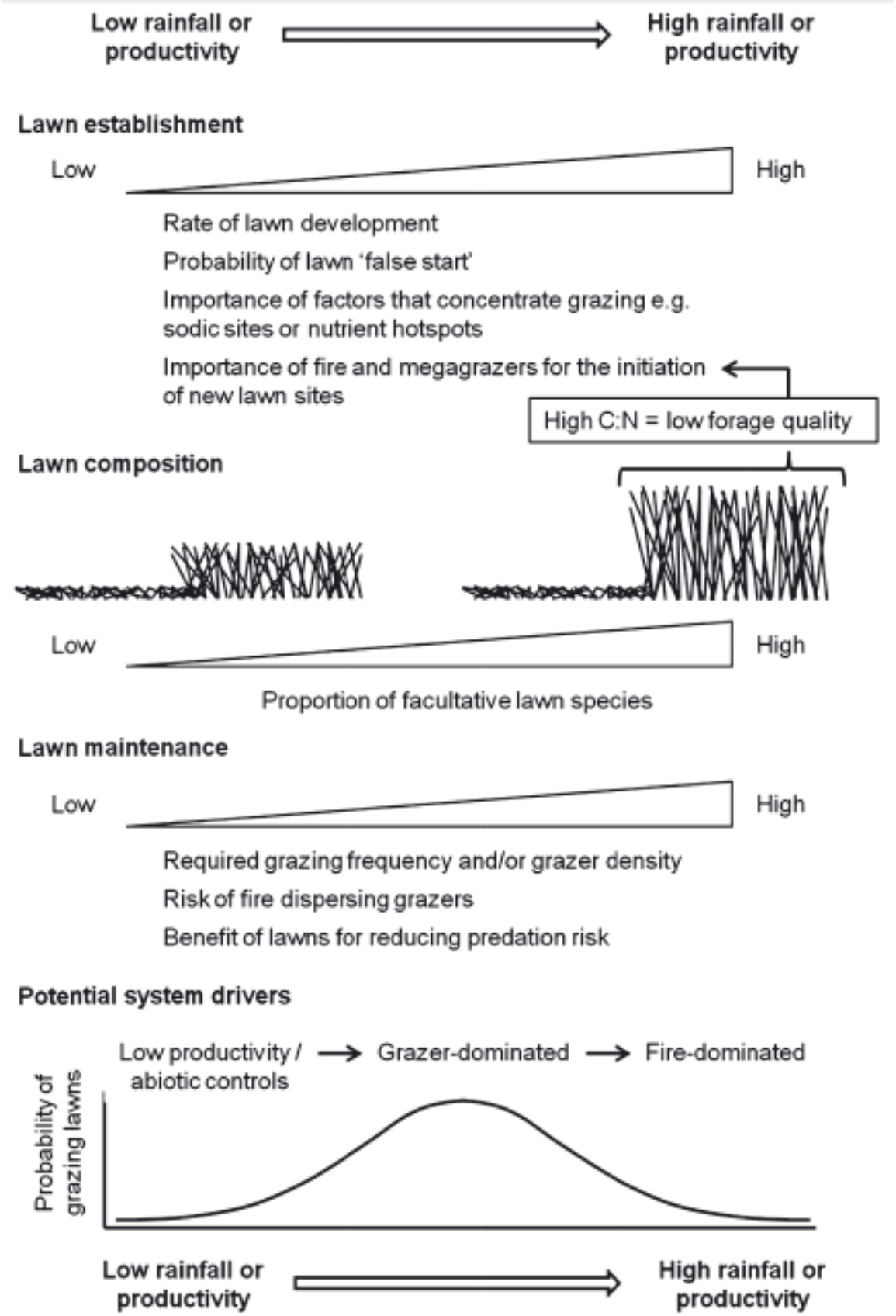

Figure 1.2 Conceptual model of grazing lawn dynamics, as determined by rainfall and productivity (Hempson et al., 2014).

intensity, as the possibility of shading by taller vegetation is increased. Lastly, Hempson et al. (2014) highlight the role that predation may play in tall grass areas of high rainfall systems, where the ability to detect a predator is compromised through reduced visibility (Riginos & Grace, 2008; Luhdo, 2016). In their work, Hempson et al. (2014) identify the multitude of factors that may influence grazing lawn development and maintenance, highlighting the complexity of grazing lawns in savanna systems.

A possible key component that may influence grazing lawn establishment is how individual grass species recover after fires in the presence of grazing, specifically the rate and nature of tillering of grasses. A high rate of tillering is an attribute associated with grasses selected for grazing (Wolfson & Tainton, 1999). Although tillering may define a grass species at a coarse scale, patterns of tillering are not purely species-specific, but are dependent on environmental conditions. The most notable differences in tillering are observed with changes in nutrient supply, moisture, temperature, and light (Wolfson & Tainton, 1999). For example, Wolfson (1989) demonstrated how nitrogen addition stimulates *Digitaria eriantha* tillering and stolon production. The timing of tiller appearance could also play a significant role in grass community compositional shifts. Frost and Robertson (1987) showed that some grass species delay their tillering until well after rains have begun (e.g. *Heteropogon contortus*) and are less affected by fires than those that initiate tillering immediately after the rains start (e.g. *Panicum maximum*). Furthermore, it has been shown that tillering is promoted at times of decreased temperature (Wolfson & Tainton, 1999). Although a decline in temperature may cause a reduction in main stem growth rates, photosynthesis continues and promotes lateral growth as a result of the greater availability of photosynthetic products that tillers have access to in the parent tiller. Therefore, the most favourable temperatures for tillering are lower than the conditions required for optimal plant growth, and thus tillering is faster in spring and autumn than in summer (Wolfson & Tainton, 1999).

Wolfson & Tainton (1999) suggest that due to several factors contributing to the rate and condition of tiller growth at once, the tillering of any given grass species will vary continuously and differ substantially between seasons. Nevertheless, the results from these studies suggest that tillering would be at its greatest when:

- Moisture content and light are adequately available for photosynthesis.
- Nitrogen is at its greatest e.g. immediately after a fire (Verweij et al., 2006, Luhdo, 2016) or when grass is maintained in a short state (McNaughton, 1984; Anderson et al., 2006).
- After the start of the rains.
- When temperatures are lower (Spring alone, as Autumn is not followed by rainfall in southern Africa).

From this, and assuming that most grazing lawn grass species adhere to the above conditions for optimal lateral tillering, it could be predicted that grazing lawns are more likely to develop in a South African savanna in a grass community that is exposed to disturbances (fire and grazing) prior to spring (August to October), which is followed by the start of the rains (September/October). It is clear that grazing lawn establishment is a complex occurrence, and as a result grazing lawns may develop under very specific circumstances. In this study I focus on the long term role that fire and grazing have on grazing lawn development.

1.4. The possible influence of grazers feeding preferences and strategies in grazing lawn development

The fact that different grazers have preferences for different sward types (and sward heights) is well known (Bell, 1970, 1971; Tomor and Owen-Smith, 2002; Verwij et al., 2006; Shipley, 2007; Arsenault & Owen-smith, 2008; Kleynhans et al., 2011; Cromsigt & teBeest, 2014). This implies that the use of the burned area by these herbivores will depend critically on the grass height. Mammalian grazing herbivores best suited to utilizing grazing lawn communities exhibit a wide mouth width to body size ratio (Arsenault & Owen-smith, 2008). However, a wide variety of grazing species have been shown to use grazing lawns in African savannas, including but not limited to white rhinoceros (Cromsigt & teBeest, 2014), warthog, and wildebeest (Kleynhans et al., 2011). Bell (1970, 1971) described grazing succession as the process of larger herbivores reducing the grass sward, which would then facilitate the feeding of smaller herbivores on the same grass sward, which would have become more accessible. While testing this theory in the Hluhluwe-iMfolozi Park of South Africa, Arsenualt and Owen-Smith (2008) found that the larger bodied rhinoceros concentrated on short grass, while impala (the smallest species),

preferred grass heights intermediate to that of zebra and wildebeest. Furthermore, they found overlap in use of grass heights between the various species. Rhinoceros, wildebeest and impala spent more time grazing on grasses 5 cm and shorter, whereas zebra spent more time on grasses taller than 20 cm.

In a separate study, Tomor and Owen-Smith (2002) showed that tssessebe (*Damaliscus lunatus*), roan (*Hippotragus equines*), Burchell's zebra (*Equus burchelli*) and Blue wildebeest (*Connochaetes taurinus*) showed preference for burnt areas as a food resource over non-burnt areas, although not equally so. However, the four species exhibited a preference for the burnt areas at different times. Therefore, after a fire when the grass is short and green we expect high utilisation by a range of herbivores. If this grass remains short then a grazing hot-spot has been initiated, and herbivory will continue at high levels. As the grass height increases we expect to selectively lose herbivores that do not prefer tall grass. At some point the grass becomes so tall that it is no longer different from the surrounding landscape, and no longer a source of patchy grazing. We also expect that some species: particularly short-grass grazers with wide mouths such as White Rhino and Wildebeest will be more effective at keeping grass short and maintaining lawns than other species.

1.5. Over-arching aim and project significance

There are few studies that examine the long term effect that both fire and grazing have on grazing lawn development. Although generally fires are homogenising agents, acting to disperse grazers through a landscape and release grazing pressure, the work from Fuhlendorf et al. (2009) and others demonstrates that smaller fires can also act to concentrate animals, and create heterogeneity. My project explores this phenomenon in the Satara area of the KNP. I used an experimental approach to determine under what conditions a small fire applied in a landscape can result in increased and continued grazer utilization (Chapter 3) and what this means in the long term for grass communities (Chapter 4), and the potential for grazing lawns at this site.

The aim of my dissertation is to determine the role that small fires and herbivory together (pyric-herbivory), play in grazing lawn development. Specifically, I want to determine the following:

i. How differences in fire size and season of burn influence grazer attraction and as such the degree of grazing intensity and duration.
ii. In addition, I want to investigate if long-term fire-grazing interactions can contribute to a change in grass community composition from one that is dominated by bunch grass species, to one that is more representative of a grazing lawn community.

I am interested in whether the pyric-herbivory mechanism can act as a catalyst for creating and maintaining grazing lawns.

1.6. Dissertation Structure

The structure of this document follows that of a conventional Masters dissertation. It consists of 4 chapters. Chapter 1 (this chapter) includes a description of the background to the project, a rationale for the research, as well as a description of the overarching aim of the project. Chapter 2 and 3 are self-contained research chapters, including extensive introductions to their respective sub-topics of the research, methodologies, as well as separate results of analyses and discussions. These two chapters are written as stand-alone chapters, intended for submission to journals, as is. For this reason, repetition of sections, paragraphs, and statements between these chapters is inevitable. Chapter 4 is an overarching conclusion, bringing the results of the chapters 2 and 3 together, and describing a way forward. Each chapter includes a list of referenced literature.

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CHAPTER 2: THE ROLE OF FIRE SIZE AND SEASON OF BURN IN MAMMALIAN HERBIVORE GRAZING ATTRACTION.

2.1. Introduction

2.1.1. Savanna ecology and pyric-herbivory

Fire, herbivory, climatic variability and soil fertility have been identified as the most important ecosystem drivers that interact and influence the dynamics of African savanna ecosystems (Huntley & Walker, 1982; Scholes & Archer, 1997; Van Wilgen et al., 2003). The individual effects of fire and herbivory specifically, have been well documented. It has been shown that fires and herbivory strongly influence system function through the alteration of the spatial heterogeneity of vegetation (Huntley & Walker, 1982; Milchunas & Lauenroth, 1993; Adler et al. 2001; Bond & Keeley, 2005; Yarnell et al., 2007), standing biomass (McNaughton, 1984;Bond & Keeley, 2005), both woody and herbaceous plant diversity (O'Connor, 1994; Jacobs & Naiman, 2008, Smith et al., 2012, Koerner et al., 2014), annual aboveground net primary productivity (Milchunas & Lauenroth, 1993), soil characteristics (McNaughton, Banyikwa, & McNaughton, 2001), and nutrient cycling (Hobbs et al., 1991; Van de Vijfer et al., 1999). However, research has primarily focused on the independent effects of fire and grazing (Fuhlendorf et al., 2009). Fuhlendorf et al. (2009) suggest that all past research unnaturally decouples fire and herbivory as disturbance factors, and further proposes that the two disturbance factors be viewed as a single ecological interaction, in which each is spatially and temporally dependent on the other. Here, fire influences grazing by changing foraging patterns and in turn, herbivores influence fire by reducing fuel loads and the capacity of fire to spread in a landscape (Archibald et al., 2005). This interaction, 'pyric-herbivory', is described as "the spatial and temporal interaction between fire and grazing, where positive and negative feedbacks promote a shifting pattern of disturbance across the landscape" (Fuhlendorf et al., 2009).

2.1.2. Grazing lawn ecology

In African savannas, with their intact indigenous herbivore communities, grazing lawns are recognised as important landscape components that increase biodiversity (Archibald et al., 2005; Cromsigt & Olff, 2008). In their work investigating the effects of hippopotamus (*Hippopotamus amphibius*) grazing in the grasslands of western Uganda, Lock (1972) was the first to conceptualize the development of grazing grass communities that were dependant on grazing activity. However, the term “grazing lawn” was first popularized by McNaughton (1984) when he described it as a community of short grass species that withstand and support heavy grazing, that provide high nutritional yield per bite (Archibald, 2008). Such lawn grass species are typically short in stature, and stoloniferous or rhizomatous. They can withstand frequent, intense defoliation and maintain a high leaf area index through horizontal growth (McNaughton, 1984). In contrast, bunch grass species form dense clumps and are only dominant under little or no grazing. Their tussock-like growth form means they are more easily uprooted by herbivores and cannot maintain sufficient aerial shoots under heavy grazing to become dominant. Many of them will even die out under frequent defoliation (e.g. *Themeda triandra*, Dankwerts, 1984). For grazing lawn persistence, frequent grazing is a necessity to prevent bunch grass species from invading the lawn community (Hempson et al., 2014).

Grazing lawns tend to develop where herbivory is frequent and regrowth rapid, and they are often associated with nutrient hot-spots (termite-mounds, old kraal sites) or water points (McNaughton, 1984; Grant & Scholes, 2006). McNaughton (1984) suggested that grazing lawns can develop in a homogeneous landscape through positive feedbacks with nutrients, although Archibald et al. (2005) demonstrated that short-grass alone is sufficient to attract grazers and create positive feedbacks with grazing. Fire is a further grazing attraction mechanism that alters the amount of short palatable grass in a landscape, and attracts herbivores onto recently burned areas (Wilsey, 1996; Guruja & Owen-Smith, 2002). Grazers are attracted to recently-burnt areas because the grass is short and nutritious, and this attraction may have a big effect on the development of grazing lawns. In particular, large/frequent fires might disperse grazers and prevent grazing lawn development, and small/infrequent fires might concentrate grazers and promote grazing lawns. Of course, this depends on various environmental factors. If enough grazers concentrate on a burnt patch, they

may be able to maintain the grass in a short “lawn-like” state. But if rainfall is high and grass grows quickly, the grass might grow up and quickly become unpalatable again. Using a simulation model, Archibald (2008) showed that significant proportions of lawns only develop under high grazer densities (200kg/ha) with infrequent fires (return period >3yrs) and in areas of low rainfall (<600mm per year), and that the extent of grazing lawns is dependent on the conditions of these three elements.

2.1.3. The role of the fire-grazing interaction in grazing lawn development

Clearly fire can play an important role in controlling the development and spread of grazing lawns, but the interaction is complex, and probably depends on the extent, timing, and frequency with which the burns occur. Although the attraction of herbivores to post-fire regrowth has been well documented (Guruja & Owen-Smith, 2002; Archibald et al., 2005; Allred et al, 2011), the consequences of this attraction for grass communities has not been sufficiently addressed. There are many reasons why herbivores move into burned areas, most of which are related to the change in vegetation structure brought about by the fire. It appears that both top-down (predator avoidance) and bottom-up (forage quality and quantity) factors are involved (Sensenig, et al., 2010; Allred et al., 2011, Luhdo, 2016). Grazer feeding strategy (Sinclair et al., 2003), timing of reproduction and lambing (Main et al., 1996), and efficiency of foraging (Wilmhurst et al., 2000)may all contribute to mammalian grazer burn preferences.

In a study investigating how animals of different body size respond to heterogeneity of forage resources in the East African savannas, Sensenig et al. (2010) conducted prescribed burns of varying sizes (1ha, 9ha and 81ha) and grain (“patchy” and “continuous”) to manipulate forage quantity and quality, and measured the response of large herbivores. All burns were done at the end of the dry season (February/March). Their findings suggest that ruminants and non-ruminants (of a significantly larger size) exhibit the same grazing preferences. Ruminants are capable of substantially greater energy intake efficiency in comparison to non-ruminants, as a result of selective retention of nutrients in their rumen. However, selective retention may also restrict non-ruminants, through their need for higher quality forage so that digestions can take place faster. As they observed higher

percentages of ruminant dung on burned areas, Sensenig et al. (2010) suggest that forage quality restricts ruminant species, whereas forage quantity restricts non-ruminants, for animals of similar body size. However, Sensenig et al. (2010) suggest that this is less important than body size in resource partitioning. Regarding fire size, Sensenig et al. (2010) admits that analysis of herbivore utilisation on different sized burns was beyond the scope of their research. Therefore, they simply note that dung count densities varied with fire size, with the lowest dung counts observed on the largest burns (81ha), and suggest that this may be due to higher quality grass being maintained on the smaller plots (Sensenig et al., 2010).

In an attempt to identify the primary mechanisms underlying fire-grazing interactions, Allred et al. (2011) showed that grazing ungulates prefer areas that have been recently burnt, over areas with greater time since fire, regardless of the size of the fire, proportion of area burnt, or the herbivore species (only Bison, *Bison bison*, and Cattle, *Bostaurus*, were studied). Time since burn was identified as the key mechanism driving the fire-grazing interaction (Allred et al., 2011). The preference for burnt areas is a result of the increased nutritional content of the post-fire regrowth (Hobbs et al., 1991). Van de Vijfer et al. (1999) showed that increased nutrient content in the post-fire regrowth of an East African savanna was the result of increased leaf to stem ratios, the re-distribution of nutrients, less above ground biomass, and rejuvenated plant material. The work of both Van de Vijfer et al. (1999) and Allred et al. (2011) show that the preference for burned areas is ephemeral, and that as grass continues to grow in the post-fire environment it becomes less nutritious, and thus less appealing to grazers.

McNaughton (1984) argued that through a positive feedback mechanism, where grazing pressure increases nutrient cycling and increases the nutrient content of the grass, grazers are attracted by both the short stature of the grass and the increased nutrient content. Furthermore, in a more recent study that involved the artificial creation of grazed patches through mowing in the Hluhlwe-iMfolozi Park of South Africa, Archibald et al. (2005) showed that all mowed sites saw a much greater and immediate increase in grazing activity when compared to un-mowed control sites.

All the research above suggests that grazers will be attracted to short grass, no matter what has caused it to be short (past grazing, fire, mowing, etc.). How long

grazers stay and graze a patch appears to depend entirely on how long it stays short, which in turn depends on both on grazing intensity and the productivity of the grasses. It is therefore important to understand under what conditions grazers can keep grass short for an entire growing season.

2.1.4. Grass, fire and grazing preferences

The fact that different grazers have preferences for different sward types (and sward heights) is well known (Bell, 1970, 1971; Tomor and Owen-Smith, 2002; Verwij et al., 2006; Shipley, 2007; Arsenault & Owen-smith, 2008; Kleynhans et al., 2011; Cromsigt & teBeest, 2014). This implies that the use of the burned area by these herbivores will depend critically on the grass height. Tomor and Owen-Smith (2002) have shown a change in grazer presence over time after a burn, and many authors have shown that herbivores eventually move off the burn to utilise other parts of the landscape. From these studies, there are various possible outcomes following a fire; these may vary depending on the season in which a fire takes place, on the size of that fire, the condition of the available forage, as well as potentially on which grazers are feeding on it. After a fire, short, nutritious grass can regrow quickly (within weeks), yet it may regrow so quickly that it becomes tall and unpalatable so that it is no longer attractive to grazers. This is likely to happen when a fire occurs close to the start of the rains in the late dry season, and if grazer density is low (Noy-Meir, 1978). Alternatively, if a fire occurs early dry season and there is sufficient soil moisture content to initiate a green flush, regrowth of new nutritious grass may happen slowly and grass may be kept short through grazing, and maintained in a productive state for an entire season. A final possible outcome is that new grass regrowth is used by grazers, but if grass does not regrow; this may result in either one of the two scenarios mentioned above eventually taking place, or the area may become degraded through over-grazing, where vegetation cover is reduced and the soil becomes vulnerable to erosion. Which of those outcomes takes place may depend on the fire season and fire size, as these influence how many animals will come to an area to graze, how attractive the new regrowth is in comparison to the surrounding unburnt matrix, and how quickly the rains cause regrowth to the point where the magnet effect is no longer apparent.

Although the magnetic effect that burned areas have on grazers is well accepted, the processes controlling how much and how long the attraction lasts still need to be elucidated (Sensenig et al., 2010, Allred et al., 2011). This is important because if the magnet effect only lasts a few weeks to a few months, then the overall impact of the fires will be to relieve grazing pressure and to promote tall-grass habitats. If the magnet effect persists through the entire growing season, then the burn site will continue to have short attractive grass in the following growing season, and this might initiate patches of short-grass grazing lawns.

2.2. Aims and predictions

In this chapter, I aim to achieve the following:

i. Investigate the effect that fire and grazing have together on the grass sward, in comparison to the effect fire has alone,
ii. Investigate how the extent of mammalian herbivore grazing attraction, intensity and duration varies with fire size and season of burn,

I predict that fire and grazing together will keep grass shorter for longer than when fire acts alone, as the attraction mechanism that fires have should encourage grazers to forage on the recently burnt areas. Furthermore, I predict that the intensity and duration of grazing will differ between different fire sizes, with the greatest grazing intensity and duration on intermediately sized burnt areas, as smaller fires are too small to attract significant grazing, and grazers will be dispersed and not concentrated enough on large burnt areas. In addition, I predict that the intensity and duration of grazing will vary with season with greatest grazing intensity after late season burns, due to the immediate green flush (provided there is sufficient soil moisture) at a time when suitable forage has been depleted. However, I expect that although grazing intensity will be lower on early dry season fires, grazing duration will be longer, as post-fire regrowth will be more nutritious than surrounding forage which will lose nutritional value over the dry season.

2.3. Methods

2.3.1. Study Area

The Kruger National Park is located in the north-eastern Lowveld region of South Africa (Figure 2.1), in the Mpumalanga and Limpopo provinces (Joubert, 1986; Van Wilgen et al., 1998). At approximately 2 million hectares in size, it is the largest protected area in the country. The park is divided into two climatic zones, north and south of the Olifants River (Venter et al., 2003). Precipitation decreases from south to north, except for the area of Punda Maria which is found at a higher altitude (Gertenbach, 1980) in the north. The northern arid bushveld zone receives between 300mm and 500mm of rainfall per year, whereas the south and central zone receives 500-700mm per year. The KNP is characterised by hot wet summers and mild, mostly frost-free winters with rainfall concentrated between October and April (Joubert, 1986; Venter et al, 2003). The KNP's geology is complex, but it is roughly divided longitudinally into granitic rocks in the west and basaltic rocks in the east, separated by a thin north-south strip of sedimentary rocks down its centre. As a result, relatively nutrient poor sandy soils and nutrient rich clay soils are found in the west and east, respectively (Joubert, 1986; Gertenbach, 1983; Venter et al., 2003).

The vegetation on the nutrient poor substrates are generally dominated by trees of the Combretaceae (e.g. *Combretum* and *Terminalia* species) and Caesalpinaceae families. Here, unpalatable grasses such as *Pogonarthria squarrosa*, *Aristida* spp., and *Eragrostis* spp. are dominant, yet occur only sparsely. *Acacia* spp. (Mimosaceae) trees and the nutrient-rich bulk grasses *Themeda triandra*, *Panicum coloratum* and *Urochloa mosambicensis* dominate the nutrient-rich basaltic soils. The northern KNP is characteristically dominated by the Mopane tree (*Colophospermum mopane*) (Gertenbach, 1983; Venter et al., 2003). The herbaceous layer of the park is generally dominated by C4 grass species (Kennedy et al., 2003). Although grazing lawns are a significant component of several southern African parks (Archibald, 2005;Cromsigt & Olff, 2008), they generally appear to be confined to sodic sites, termite mounds and hippo grazing areas in Kruger (Gertenbach, 1983; Naiman et al., 2003; Grant & Scholes, 2006). My experiment took place in the *Sclerocarya birrea*/*Acacia nigrescens* landscape of Satara in the central KNP (Figure 2.2). This area is located on basaltic soils, and reflects

intermediate levels of rainfall (approx. 550mm/ year), relative to the rest of the KNP. The site represents moderate soil fertility, moderately low rainfall, and a significant grazer presence (relative to within KNP) and therefore it meets the environmental criteria described by the model created by Archibald et al. (2008) under which we expect grazing lawns to develop.

2.3.2. Study Design

To allow for comparison of results from differently sized burn plots and to represent the variability at different scales, sampling effort was increased in larger plots. My sampling design centres on a 0.25ha sub-plot, the size of our smallest burn. Each intermediate fire had four subplots, while large burns had nine subplots for sampling. Sub-plots were evenly spaced within each burn plot (Figure 2.3). Table 2.1 shows the number of replicates, subplots and transects per treatment for each season of burn.

Table 2.1 The total number of replicates, sub-plots, and transects for each plot for both early and late season burns.

	Early Season Burns			**Late Season Burns**		
Plot	*Replicates*	*Sub-plots*	*Transects*	*Replicates*	*Sub-plots*	*Transects*
0.25ha	4	1x 4 = 4	8	4	1x 4 = 4	8
5ha	4	4x4 = 16	32	3	3x4 = 12	24
25ha		N/A		2	2x9 = 18	36
Control	4	4x9 = 36	72	Control plots shared between seasons		

Data on grass height, grass biomass and dung counts were collected along two 50m transects (2m wide belt transects in the case of dung sampling) in each sub-plot. In addition, a 1m x 1m grazing exclusion plot was placed in the centre of each sub-plot, allowing for me to determine the effect of fire alone. We had a total of 36 control sub-plots which were distributed in four 25ha plots located throughout the experimental site. This gave an accurate depiction of both within-plot and between-plot variability in the control landscape. We were unable to use fire breaks to protect experimental burn patches, as the new growth in these fire breaks would attract herbivores and

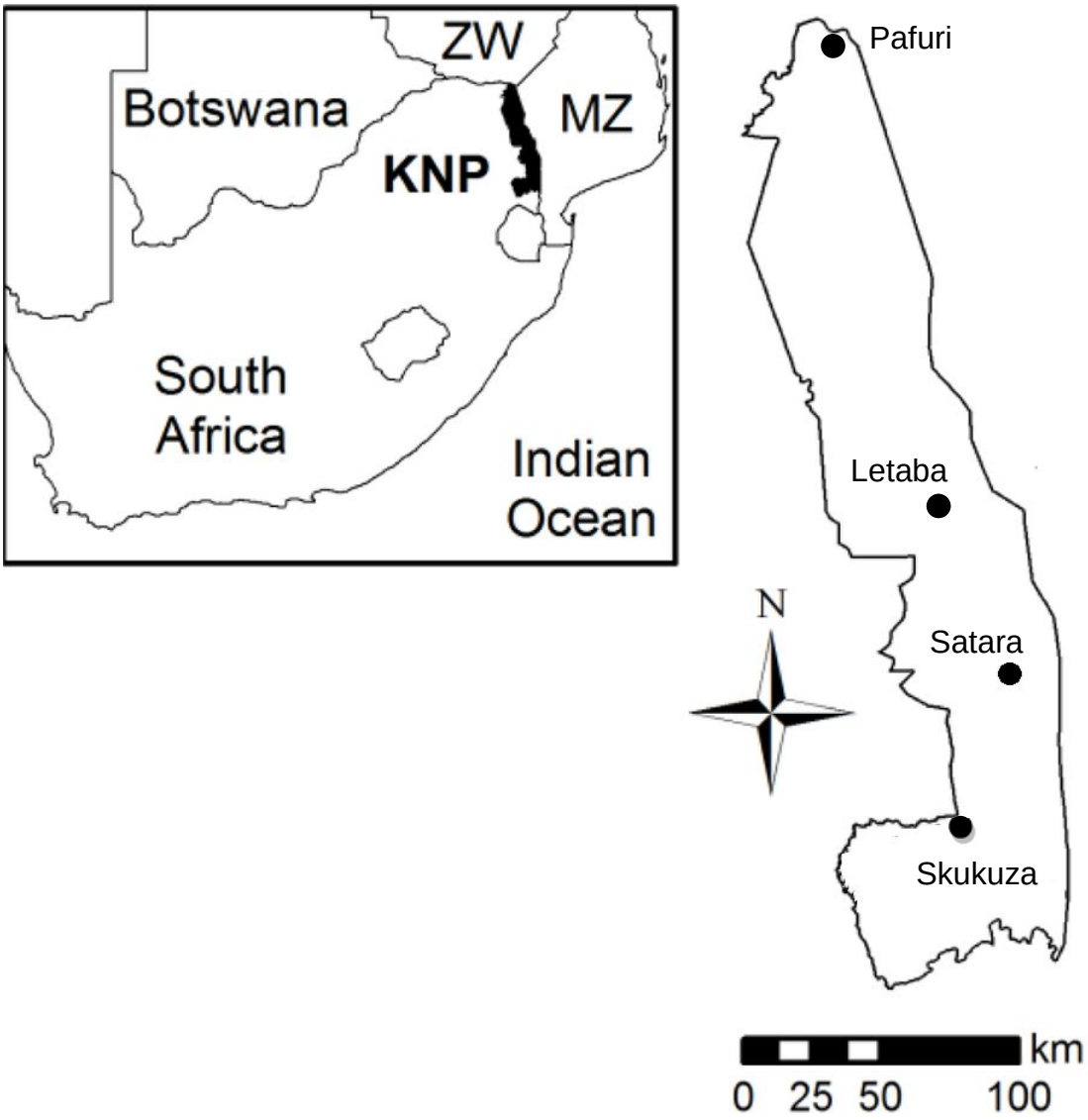

Figure 2.1 Map of the Kruger National Park located in the north-eastern corner of South Africa. Satara is located in the central region of the park (adapted from Colgan et al., 2012).

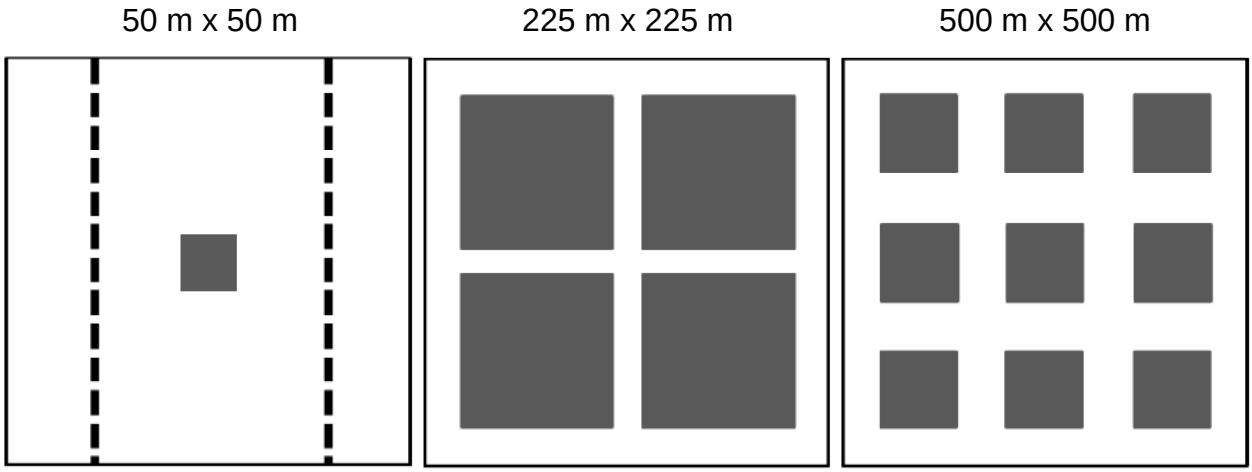

Figure 2.2 The arrangement of transects (dashed lines) and the fixed plot (centre square, left) within a 0.25ha plot (equivalent to a sub-plot; left), and the arrangement of sub-plots within the 5ha (middle) and 25ha and control (right) plots. The illustration is not to scale.

confound our results. Instead, all experimental burns took place within fire management blocks used by KNP management within the Satara region. Although we attempted to exclude and/or suppress all management, natural and accidental fires from the study site for the duration of research, one natural fire burnt a section of the study site and several small management fires occurred within close vicinity to the site. These fires were approximately 1 kilometre from one of the experimental burns, and were assumed to have not affected the results substantially.

Data were collected once pre-fire and at several intervals post-fire to reflect change over time, and finally at the end of the following growing season. Grass height and biomass were recorded at 5m intervals along the transects (22 points per sub-plot) to provide an indication of change in grazing intensity over time. Grass height and biomass were also measured in the grazing exclusion plots. A single grass height measurement was taken using a measuring stick with 5cm interval markings, and four biomass readings were recorded with a disc pasture meter to determine an average. Grass biomass was calculated with the calibration developed by Trollope & Potgieter (1986) for the KNP. The data from the grazing exclusion plots represent a "grazing-off" scenario, either in the presence or absence of fire, allowing for the determination of grass regrowth (or lack thereof).

Dung counts were used to provide an indication of the abundance and frequency of patch visitation by mammalian herbivores, i.e. grazer attraction. Dung counts were made by two observers along the original transects, and observations restricted to a 4m wide belt transect (400m^2 per sub-plot, representing 16% of each sub-plot). The frequency of dung piles and their respective species were recorded, and animal observations used to validate the data. Once counted, dung was squashed and/or spray-painted to prevent recounts in subsequent data collection bouts. Dung counts have been proven useful in several studies (Archibald et al., 2005; Sensenig et al., 2010; Allred et al., 2011), but there are several problems. Some species that defecate in middens, such as white rhinoceros (*Ceratotherium simum*) are less likely to defecate on transects, and the wide array of species that do defecate on transects have different body sizes, dung amounts and sizes. Their differences in dung quantity will therefore not reflect visitation rates perfectly (Archibald et al., 2005; Sensenig et al., 2010). For this study, analysis of dung count data (dung prevalence) were restricted to mammalian herbivores, specifically grazers and mixed feeders.

Browsers were excluded as they are not expected to have a significant effect on grass regrowth. Analysis will be restricted specifically to the Burchell's zebra (*Equus burchelli*, bulk feeder), impala (*Aepyceros melampus*, mixed feeder) and Blue wildebeest (*Connochaetes taurinus*, highly selective grazer). These three species represent the main grazers found in the study landscape.

2.3.3. Sub-sampling of landscape data

After the late season fires had been applied, I found that there was not enough time in a given month to sample from all burn plots of both the early season and late season. Therefore, sub-sampling took place over several sampling periods in this study. This was done to accommodate full sampling of a given season (early or late dry season) in a single month, yet maintain sampling of the other seasonal data. In the months following the application of the late season burns, sub-sampling was alternated between sites burned in the early season, and those in the late season. That is, in a given month for example, all plots and sites were sampled for sites burned in the early season, whereas the late season plots were sub-sampled. In the following month, the opposite would be done. However, due to other time constraints, sampling could not be conducted in every month for both seasonal samples. Sub-sampling methods differed depending on plot or fire size, and the data being collected. The smallest plots (0.25ha) were small enough so that all grass height data was collected. On the 5ha plots, all sub-plots were sampled from, however data was only collected from the first 5 points per transect (i.e. half the transect). The same practice was performed on the 25ha plots, however only 5 of the 9 sub-plots were sampled from, namely the 4 corner and centre sub-plots. In the case of dung sampling, sub-sampling protocol followed the same method as in the case of grass height data, however the entire belt transect was sampled from. For logistical reasons, dung data could not be collected in November and December of 2013 for the EDS plots.

2.3.4. Data analysis

All data analysis was conducted using the R open source statistical software (Version 3.2.1). All statistically comparable groups were tested for normality using the Shapiro-Wilks test and the Kolmogorov-Smirnov test (in the case of large data

sets). The Pearson's test was used to determine the significance of correlations. I chose to use grass height as my response variable in all analyses involving grazing intensity, because this is what grazing animals are responding to when making foraging decisions (Bell, 1970; Arsenault& Owen-Smith, 2008), and because grass height is directly correlated with both grass greenness, and percentage nitrogen content (Luhdo, 2016). Because there was a strong, positive correlation between grass height and biomass ($t = 31.397$, $df = 356$, $p < 0.001$, $r = 0.857$, Figure 2.5), grass height was used instead of biomass as an indicator of grazing intensity. The plots presented in the results exhibit change over time by month. Where sampling did not take place in a given month, it is indicated with a hash following the name of the month(s) (e.g. Oct - Nov#). This was done to show gaps in data for ease of plot interpretation. Where sub-sampling took place, an asterix is used (e.g. Dec*). All figures are expressed using means (m) and standard errors (SE).

2.3.4.1. Considering seasonal differences in grazer attraction and grazing intensity

I compared post-fire grass height and dung prevalence overall (regardless of time) between EDS and LDS burns of differing sizes (0.25ha, 5ha, and 25ha). This comparison shows which treatments have the shortest grass, and which have the highest dung prevalence. This gives a general indication of whether mammalian grazer species show a feeding bias towards a particular fire size and for areas burned either in the early or late dry season. For all of these analyses, the non-parametric Kruskall-Wallis test was used to determine if differences existed between groups, and the Dunn's Test (*dunn.test* R package) as a post-hoc used to determine which groups differed from each other.

2.3.4.2. Investigating change over time

To determine whether there was any difference between the effect of fire alone and the effect of fire and grazing together on grass height, I compared grass heights in both the EDS and LDS between grazed (Burn + Graze) treatments and un-grazed (Burn + No Graze) exclosures (regardless of fire size) in each individual sampling period (month, ISP) over the duration of the experimental period. A similar analysis was conducted on the dung count data. However, comparison in each ISP was

conducted between dung prevalence on the burned plots and the unburned (No Burn + Graze) plots. From this one can determine if grazers are more attracted to burned areas, and for how long the grazing attraction mechanisms persists. All comparable groups were tested using the Wilcoxon rank-sum test, and data were represented in line graphs over time.

Linear mixed effect models were used to explore the role of various factors in changes in grass height and dung counts over time (lme4 R package). To show change over time, and to allow for adequate comparison between seasonal data, analysis was conducted using data from three intervals in the experiment: Pre-fire (April 2013 for EDS burns and September 2013 for LDS burns), Mid-growing Season (November – December 2013), and at the end of the growing season (April 2014). This analysis was conducted for both grass height and dung counts to show changes in the degree and extent of burned area utilization. A final model was used to show the influence that the timing of the rains had on grazing of burnt areas. The data used for this model only included data since the time of the start of the rains (October onwards).

The following variables were considered as potential factors for the various models that were used, with explanation where necessary:

Fixed effect factors:

i. Season of Burn (Season)
    a. Data grouped based on the timing of the year for which the plots were burned (i.e. Early Dry Season (EDS) and Late Dry Season (LDS)).
ii. Treatment (TRMT)
    a. Groups of treatment application type (categorical factor) per plot, as follows:
        i. In the case of analysing change in grass height over time Burn + No Graze (Grazing Exclosure on burn plots), No Burn + Graze (Control plots), No Burn + No Graze (Grazing Exclosure on Control plots).
        ii. In the case of analysing change in dung occurrence over time: Burn + Graze and No Burn + Graze
iii. Size of fire (SOF)

a. Categorical factor indicating the various sizes of fires applied: 0.25ha, 5ha and 25ha. Note that the 25ha are omitted from the early season analyses as there were no plots this size.
b. As only a single unburnt control size was sampled from, each control plot was sub-sampled for data analyses in order to have a mirrored control for each experimental fire size. One, four, and all nine sub-plots were randomly chosen from each control plot in order to represent a control for the 0.25ha, 5ha and 25ha burn plots, respectively.

iv. Time since rain (TSR)
    a. A numerical value associated with each individual sampling period since the start of the rains (continuous factor). All data prior to the rains are excluded.

Random effect factors:

i. Plot (A particular plot, associated with size of fire and season of burn)
ii. Site (A particular sub-plot within a plot, e.g. Early Season 5ha plot, subplot A)
    a. Site was embedded in Plot for all models. For convenience, these are depicted in the model tables shown in the results.

To test for the effect of size, season and treatment on the grazers ability to keep the grass short I ran a linear mixed effects model with grass height in April as the response variable, treatment, season and size as fixed effects, and plot and site as random effects. I explored various combinations of effect variables and used an information theoretic approach (Burnham & Anderson, 2002) to assess the best model.

2.4. Results

2.4.1. The relationship between dung counts and grass height

My data suggest there is strong evidence to support the idea that impala ($t = -4.465$, $r^2 = -0.276$, $p < 0.001$), wildebeest ($t = -3.010$, $r^2 = -0.189$, $p = 0.003$), and zebra ($t = -5.484$, $r^2 = -0.332$, $p < 0.001$) all show preference for shorter grass over longer grass (Figure 2.3). Specifically, zebra appear to have grazed taller grass more than either wildebeest or impala. Traditionally these three species are viewed as bulk, selective, and mixed feeders, respectively. The trends suggest that both impala and wildebeest select for the shortest of grasses, with both exhibiting a maximum dung prevalence at grass heights of 5-10cm. The trend for impala is arguably more selective for shorter grasses than in the case of wildebeest. In contrast, zebra appeared to be actively selecting for the taller grass plots (maximum dung counts at 10-15cm grass height). Above 25cm the "attractive" effect of short grass is much reduced and above 30cm is totally gone.

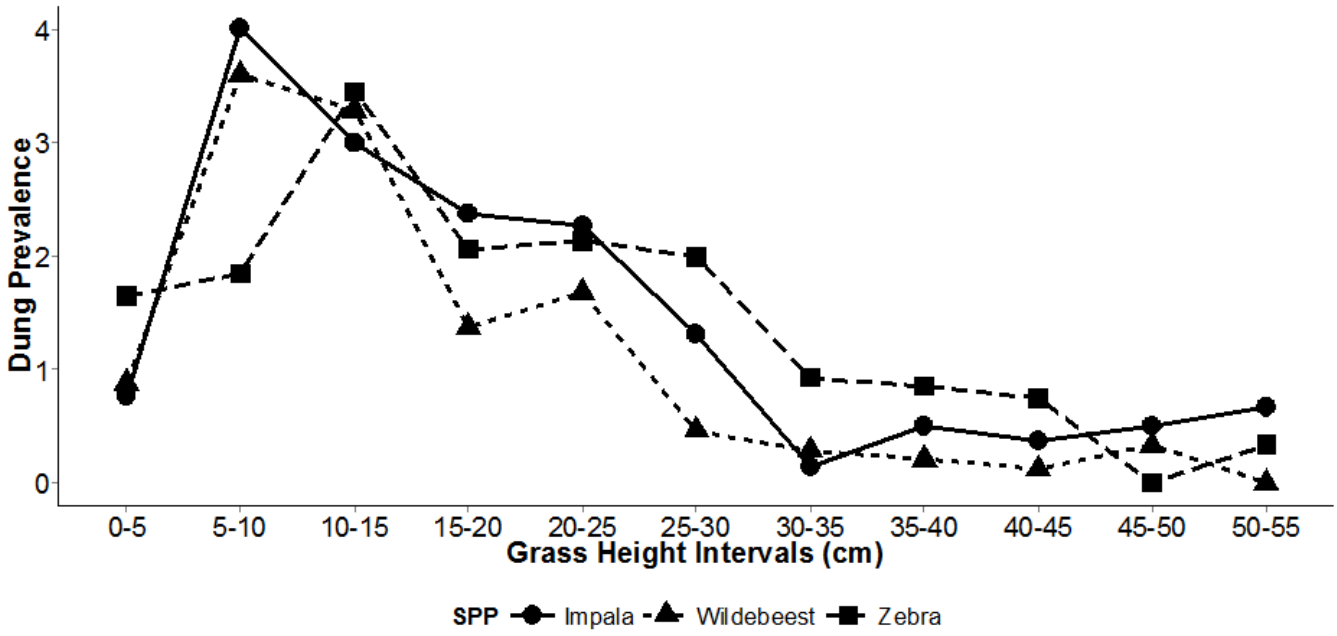

Figure 2.3 The relationship between grass height and dung prevalence (mean dung count) to post-fire regrowth of three grazing mammalian herbivores namely; impala, Burchell's zebra and Blue wildebeest.

2.4.2. Patterns of grazer utilisation of the burn plots

On the EDS plots after the application of the fires, dung prevalence decreased on the unburned plots and increased on the burned plots (Figure 2.4). Dung counts than continued to be higher on burned plots until September, when dung on burned plots decreased. This suggests that grazers may have been visiting burned plots more frequently than the unburned plots during the first few months. However, the September dip suggests that the magnetic effect of the burned plots subsided in the late dry season, between July and September. Despite this dip, there was a large increase in dung prevalence on burned plots several months later in December (Fig. 2.4). This spike in dung counts occurred only a few months after the rains, thus indicating a potentially substantial role that the rains have in promoting grass growth and grazer attraction. This effect is once again observed to be ephemeral, as dung prevalence decreased by April 2014. On the LDS plots, dung counts did not differ between burned and unburnt plots until after the rains when there was higher dung on the burn plots (November) (Fig. 2,4). Dung prevalence decreased on both plots from this point onwards, however dung counts remained higher on the burned plots until April 2014 (Fig. 2.4).

2.4.3. Factors driving grazer utilisation of the burn plots

Mixed effects models indicate that grazer utilisation was uniform across all plots before the experiment was applied (Table 2.1). After the first rains (November) there was significantly more dung on the burned plots, and significantly more dung on the 5ha plots but there was no season effect (Table 2.1). At the end of the growing season the treatment effect had disappeared but it did appear that grazers were using the small burns more than the other two sizes (Table 2.1).

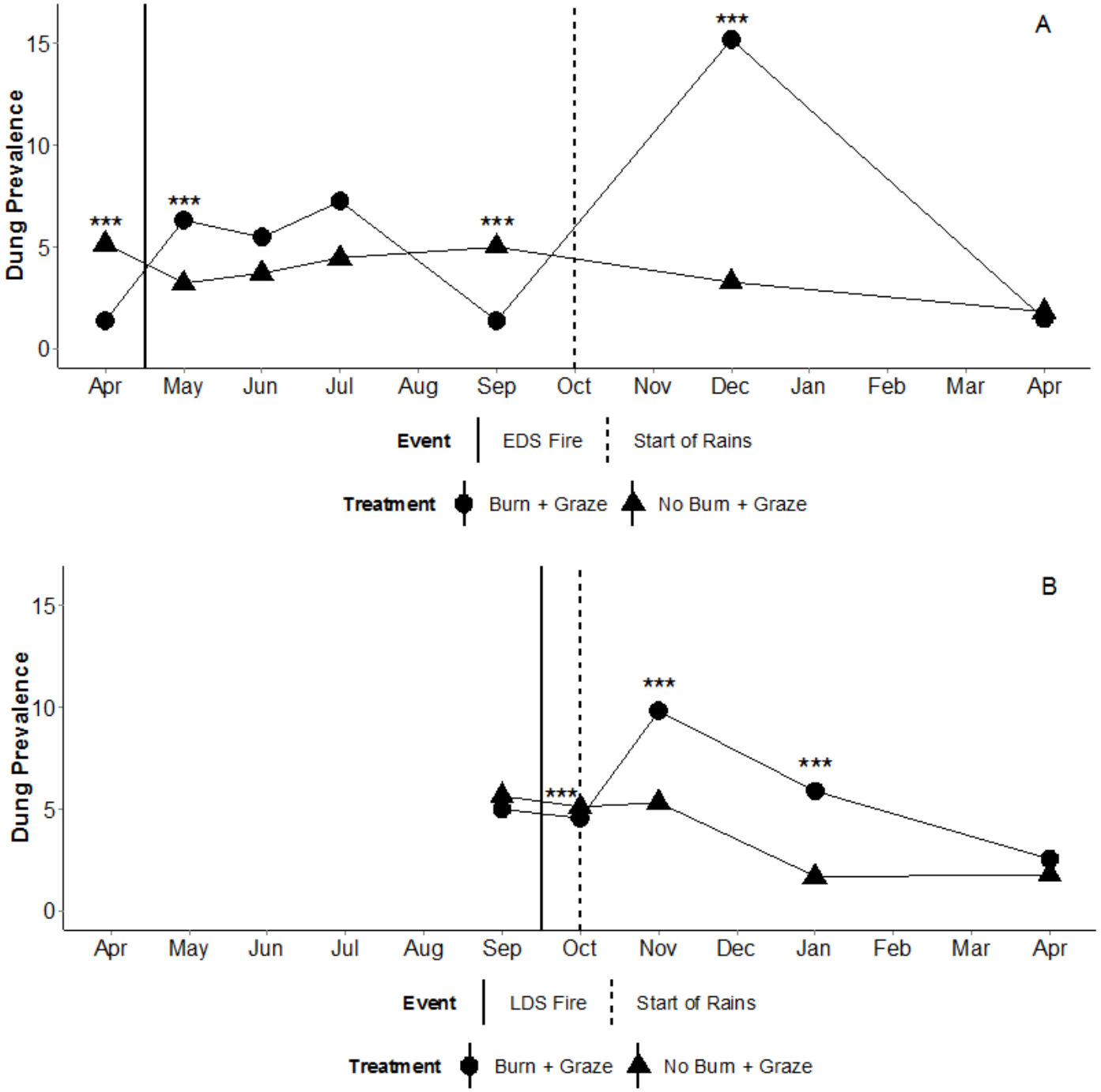

Figure 2.4 Trend of dung prevalence (mean dung count) burned (Burn + Graze) and unburned (No Burn + Graze) plots after the application of early (A) and late (B) dry season burns. Asterix's above points indicate significant difference between treatments in a given sampling period (month).

Table 2.1 Estimated dung count coefficients from linear mixed effects models used to determine the influence of factors on dung prevalence in areas burnt in the early dry and late dry season at 3 stages (months) of the experiment (Pre-fire conditions, after the rains, and the end of the growing season). Model categorical fixed factors include season of fire application (early dry season or late dry season), treatment (unburned, and burned plots and grazing exclosures, respectively), AND size of burn (0.25ha, 5ha, 25ha). Early Dry Season and 0.25ha sized plots are the reference categories in each model. Factors exhibiting a t-value greater than 2.00 are considered significant.

Pre-fire	**Estimate**	**SE**	**t-value**
Intercept	1.556	0.721	2.159
Late Dry Season	0.468	0.427	1.095
Burn + Graze	-0.664	0.685	-0.970
5ha	0.067	0.480	0.140
25ha	-0.146	0.504	-0.289
After first rains (November)	**Estimate**	**SE**	**t-value**
Intercept	0.273	0.975	0.280
Late Dry Season	0.667	0.472	1.412
Burn + Graze	3.156	1.068	2.954
5ha	1.154	0.444	2.601
25ha	0.716	0.481	1.490
End of growing Season (April)	**Estimate**	**SE**	**t-value**
Intercept	0.982	0.3223	3.046
Late Dry Season	0.214	0.192	1.116
Burn + Graze	0.148	0.306	0.484
5ha	-0.545	0.225	-2.423
25ha	-0.687	0.242	-2.836

2.4.4. Temporal effect of fire and grazing on grass heights

On the early dry season burn plots (regardless of burn size), the fire reduced grass height. Grass heights remained shorter on the burned and grazed plots (EDS Burn + Graze) than in the exclosures (EDS Burn + No Graze) for several months after the application of the burns (Figure 2.5). However, after January the burned and grazed treatment grew tall and in April 2014 (end of measurements), grass heights on these plots (m = 42.782 cm± 0.649 SE) far exceeded ($W = 7183.5$, $p < 0.001$) those in the grazing exclosures (m = 27.500 cm± 1.971 SE). In the case of the late dry season burn plots, grass heights increased immediately after the start of the rains on both the burned plots (LDS Burn + Graze) and grazing exclosures (LDS Exclosures). However, the grass heights in the grazing exclosures remained significantly ($p > 0.05$) taller than on the grazed burn plots throughout the experiment.

2.4.5. Experimental factors influencing grass height over time

Before the burns were applied it appears that the late dry season plots had shorter grass than the early dry season plots overall, and that the burn plots had taller grass than the no burn plots (Table 2.1). None of these differences should invalidate our experiment. After the application of the burns the influence of various experimental factors appeared to change as time progressed after the application of the burns (Table 2.1). A fire size effect was never significant. Immediately after the first rains (November), there was a strong treatment affect. As expected the burned sites had shorter grass than the unburned sites (It was ~17cm shorter for Burn + Graze and ~9cm shorter for the burn alone indicating that grazing was keeping the grass short). The unburned + grazing had ~2cm shorter grass than the unburned – grazing. However, there was no significant effect of season at this time.

By the end of the growing season the effect of the fire on grass height was gone – grass height on both the burned treatments was not significantly different from that of the unburned. The unburned and un-grazed treatment did have significantly taller grass however. Lastly, the effect of plot size was never found to be a significant factor, and hence was excluded from all models.

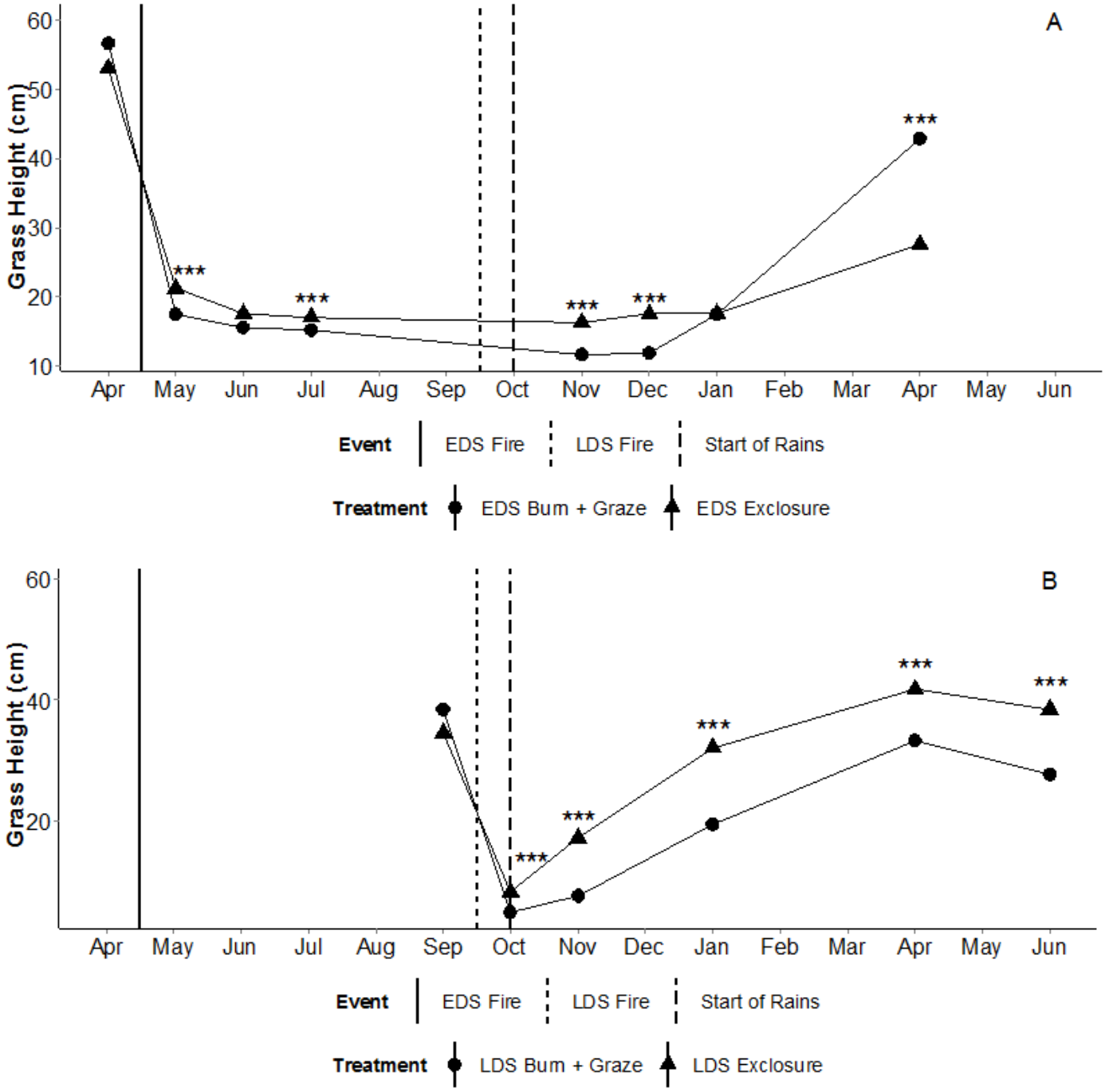

Figure 2.5 Trend of grass regrowth in the presence (Burn + Graze) and absence (Exclosure) of gazing after the application of early (A) and late (B) dry season burns. Asterix's (*) above points indicate significant difference between treatments in a given sampling period (month).

Table 2.2 Estimated grass height (cm) coefficients from linear mixed effects models used to determine the influence of factors on grass height in areas burnt in the early dry and late dry season 3 stages (months) of the experiment (Pre-fire conditions, after the rains, and the end of the growing season).Model categorical fixed factors include season of fire application (early dry season or late dry season) and treatment (unburned, and burned plots and grazing exclosures, respectively). Early Dry Season, 0.25ha sized plots, and No Burn + No Graze are the reference categories in each model. Factors exhibiting a t-value greater than 2.00 are considered significant.

Pre-fire	**Estimate**	**SE**	**t-value**
Intercept	44.104	4.250	10.379
Late Dry Season	-15.182	1.021	-14.876
Burn + Graze	10.980	3.944	2.784
Burn + No Graze	8.199	4.327	1.895
No Burn + No Graze	-4.263	1.848	-2.307
5ha	-3.217	4.483	-0.718
25ha	0.432	4.970	0.087
After rains (November)	**Estimate**	**SE**	**t-value**
Intercept	26.069	1.757	14.835
Late Dry Season	-0.189	0.592	-0.319
Burn + Graze	-16.580	1.650	-10.049
Burn + No Graze	-8.615	2.047	-4.209
No Burn + No Graze	2.639	1.212	2.177
5ha	0.337	1.863	0.181
25ha	-0.846	2.164	-0.391
End of Growing Season (April)	**Estimate**	**SE**	**t-value**
Intercept	35.031	1.846	18.982
Late Dry Season	-0.429	0.684	-0.628
Burn + Graze	2.365	2.439	0.969
Burn + No Graze	2.220	2.820	0.787
No Burn + No Graze	8.301	1.399	5.929

2.4.6. Grazer utilisation and grass height following the first rains.

As would be expected there was a rapid increase in grass height and decrease in grazer utilisation after the first rains (Figures 2.5 and 2.4). To test whether the rates at which this happened were influenced by our treatment I ran further mixed effects models with time since first rainfall as a continuous predictor variable. Time since last rain shows a strong positive and negative effect on grass height and dung prevalence, respectively (Table 2.3). However, the treatment effect persists – indicating that burned and grazed sites grew back more slowly than sites that were burned and not grazed.

2.4.7. Post-fire seasonal treatment comparison

No seasonal difference was observed in grass height on the smallest burns (0.25ha, Figure 2.6). However dung prevalence was significantly greater ($p = 0.02$, $Z = 2.844$) on the LDS burn ($m = 2.875$ cm± 0.597 SE) than what it was on the EDS burns ($m = 1.472$ cm± 0.389 SE), suggesting that grazers were visting the small LDS treatments more frequently. There was strong evidence for more dung ($m = 2.958 \pm 0.296$ SE) and shorter grass ($m = 14.090$ cm± 0.376 SE) on the LDS 5ha burn plots compared to 5ha EDS plots ($p < 0.001$, $Z = 3.595$). Furthermore, both the 25ha treatments and 0.25ha treatments exhibit statistically different dung and grass heights that are lower and greater than that seen on the LDS 5ha burns, respectively. Regarding the unburned control treatments (No Burn + Graze), a statistically significant difference was observe in grass height ($p = 0.004$, $Z = -2.651$) between the EDS ($m = 32.536$ cm± 0.310 SE) and LDS ($m = 30.687$ cm± 0.199 SE) treatments, however this difference was small and probably biologically insignificant. Dung prevalence was equal between the seasonal treatments of the unburned plots ($p = 0.082$, $Z = 1.397$).

Table 2.3 Estimated grass height (cm, top) and dung count (bottom) coefficients from linear mixed effects models used to determine the influence of the start of the rains (October) on several experimental factors. Model categorical fixed factors include season of fire application (early dry season or late dry season), treatment (unburned, and burned plots and grazing exclosures, respectively), size of burn (0.25ha, 5ha, 25ha), species of grazers (impala, Blue wildebeest, Burchells zebra), and Time Since Rain (TSR). Factors exhibiting a t-vale greater than 2.00 are considered significant.

Grass Height	**Estimate**	**SE**	**t-value**
Intercept	21.5519	1.2423	17.35
Late Dry Season	0.4585	0.3975	1.15
Burn + Graze	-10.9231	1.6478	-6.63
Burn + No Graze	-5.6902	1.8010	-3.16
No Burn + No Graze	2.3058	0.7574	3.04
Time Since Rain	2.7261	0.0428	63.70
Dung Prevalence	**Estimate**	**SE**	**t-value**
Intercept	2.08025	0.51252	4.059
Late Dry Season	-0.01454	0.24356	-0.060
Burn + Graze	1.38670	0.53788	2.578
5ha	0.11496	0.20299	0.566
25ha	-0.29533	0.21379	-1.381
Wildebeest	-0.11611	0.14658	-0.792
Zebra	0.01896	0.14658	0.129
Time Since Rain	-0.28182	0.02616	-10.771

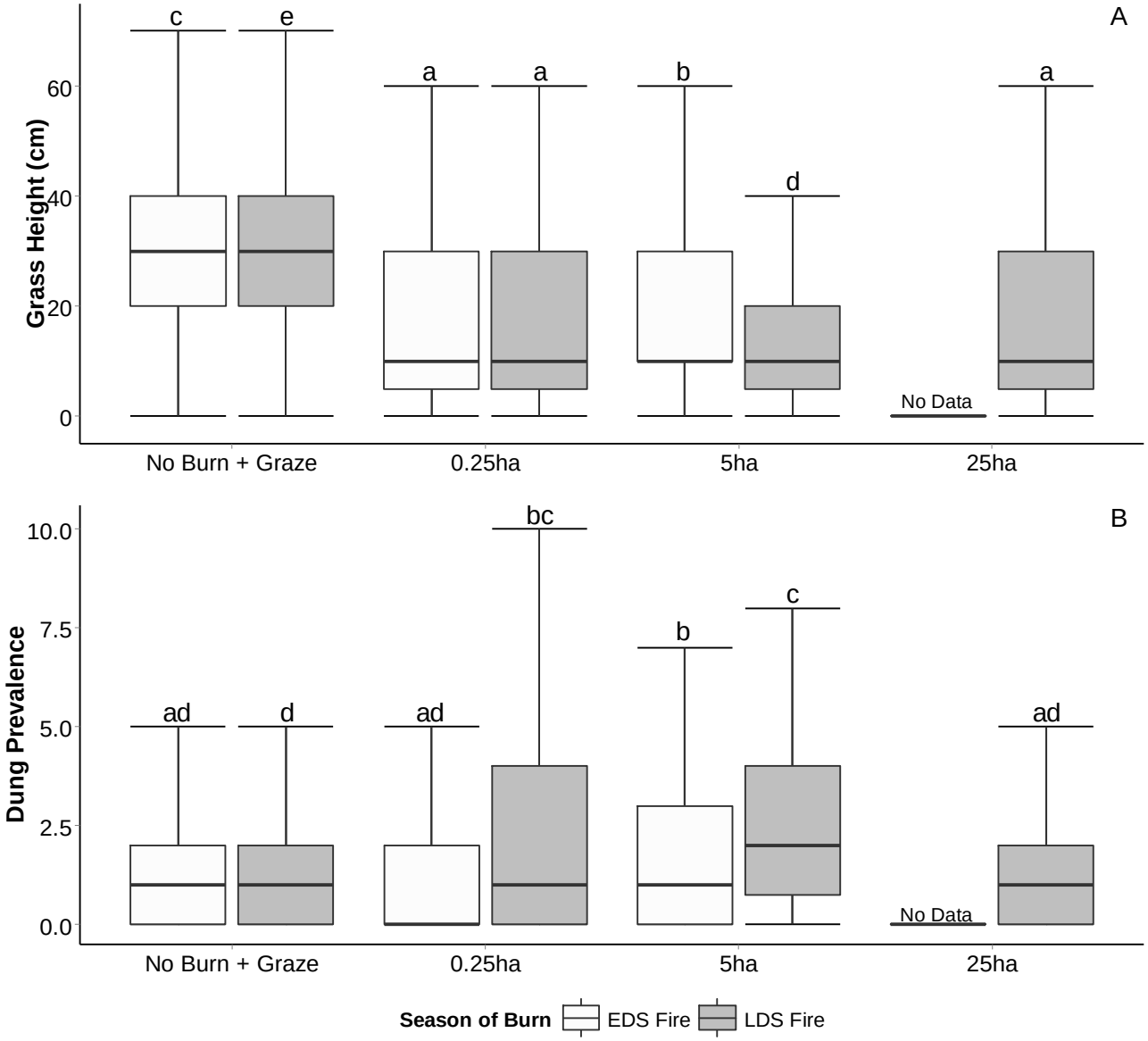

Figure 2.6 The overall comparison of grass height (A) and dung prevalence (B) among seasons and treatments for all post-fire data. The letters above each boxplot indicate similarity between each group. Groups that exhibit the same letter(s) are statistically similar ($p > 0.05$).

2.5. Discussion

The fire-grazing interaction plays an important role in the fire-driven savanna biome (Archibald et al., 2005; Leonard et al., 2010; Sensenig et al., 2010; Allred et al., 2011), and if applied in a controlled fashion it could potentially be a mechanism for initiating grazing lawn development at sites which are dominated by tall grass, given that herbivores can be attracted over extensive periods. By quantitatively measuring the influence that fires of different sizes and season of burn have on grazer attraction, as well as the temporal effect that grazers have on forage quantity after these fires, I have identified how grazers interact with fires of different seasons and sizes. This landscape level experiment supports already established results that fire acts as a strong magnet for grazing attraction, and that the time since a burn heavily influences selection of burned areas. These finding could have implications pertaining to grazing lawn development

2.5.1. Change in grazer attraction and grazing intensity over time

As I hypothesized, it is apparent that fire and grazing together keep grass shorter and for longer than when fire is acting alone as a disturbance mechanism (Figure 2.4). This was evident for both the EDS and LSD fires, however it could be argued that grass remained shorter for longer on the EDS burns than on the LDS burns. Although it is apparent that fire and grazing maintained a short grazed patch for several months, and that grazers are perhaps more attracted to burned areas after the start of the rains, it is important to note that this attraction was only ephemeral, and essentially a short grazed patch was not maintained for longer than a single growing season. Research by Allred et al. (2011) identifies time since burn as the key mechanism driving the fire-grazing interaction. The initial preference for burned areas is, in part, a result of the increased nutritional content of the post-fire regrowth (Van de Vijfer et al., 1999; Hobbs et al., 1991). However, Allred et al. (2011) infer that this preference is only ephemeral, and that as grass continues to grow in the post-fire environment it becomes less nutritious (Allred et al. 2011), and thus less appealing to selective grazers. My data confirm this, with all grazers showing a preference for grass < 30cm tall, and wildebeest and impala for grass <15cm tall (Figure 2.3). A trade-off can exist where the greatest quality food is found in the areas with the least amount of food (i.e. high quality but short grass).

Nitrogen has been shown to be particularly important for grazing lawn maintenance, as it is an important attractor for grazers and it's presence is enhanced by grazing (McNaughton, 1984; Anderson, Fuhlendorf, & Engel, 2006; Verweij et al., 2006; Coetsee et al., 2010). In research that ran parallel to my work on the same burns in Satara, data from Luhdo (2016, Figure 2.9) shows that foliar nitrogen content (NH_4) increased immediately after the burns. On the EDS treatments, nitrogen remained high for seven months after the burns, whereas for only one month after the LDS fires. The decrease in nitrogen for both seasonal treatments coincides with the timing of the rains. In their research using macronutrients (N, P, K, Ca and Mg) as indicators of forage quality, Van de Vijver et al. (1999) showed that, although high levels were exhibited immediately post-fire, this condition was short-lived as all macronutrients had decreased to the same levels as was evident in fire excluded areas within three months of the initial burns. As was also found on our experiment, this reduction in foliar nutrients was directly correlated with grass height.

I predicted that grazing pressure would be ephemeral. However, when grass did begin to regrow on the EDS burns, the rate of regrowth rapidly exceeded grass regrowth rates in the grazing exclosures. It is known that disturbances can stimulate grass regrowth (McNaughton, 1979; Tainton, 1999), and it could therefore be assumed that in my experiment fire and grazing together, in conjunction with rainfall, stimulated faster grass regrowth in this fashion. To my knowledge, no published work has identified such a phenomenon where two disturbance factors working in conjunction increase grass regrowth rates to a speed faster than a single disturbance (e.g. grazing) may do this. It also demonstrates that the continuous heavy grazer presence on the sites throughout the dry season did not prevent high grass growth rates. I suggest that a focussed study investigate this occurrence.

2.5.2. Timing of the rains & the role of the dormant dry season

The timing of rainfall and its subsequent effect on the fire-grazer interaction is a component that has not been investigated before. My results have shown that in the case of fires burned in the EDS, although grazer attraction is ephemeral, the dormant winter period allows for grass to remain short even after grazer visitation has subsided, and until the rains start. At this point, the start of the rains promoted the green flush which allowed for the rejuvenation of grazing on the EDS burn

treatments that otherwise would have been left to regrow, allowing for the maintenance of a short grazed patch for much longer than that observed on LDS fires. However, the start of the rains also marked the “beginning of the end” of the short grazed patches. Soon after the rains, grass started to re-grow too rapidly for the number of grazers present to keep it short, which eventually saw grazers moving away from the burned plots to find suitable forage elsewhere in the Satara landscape where grass quality would have also improved after the rains.

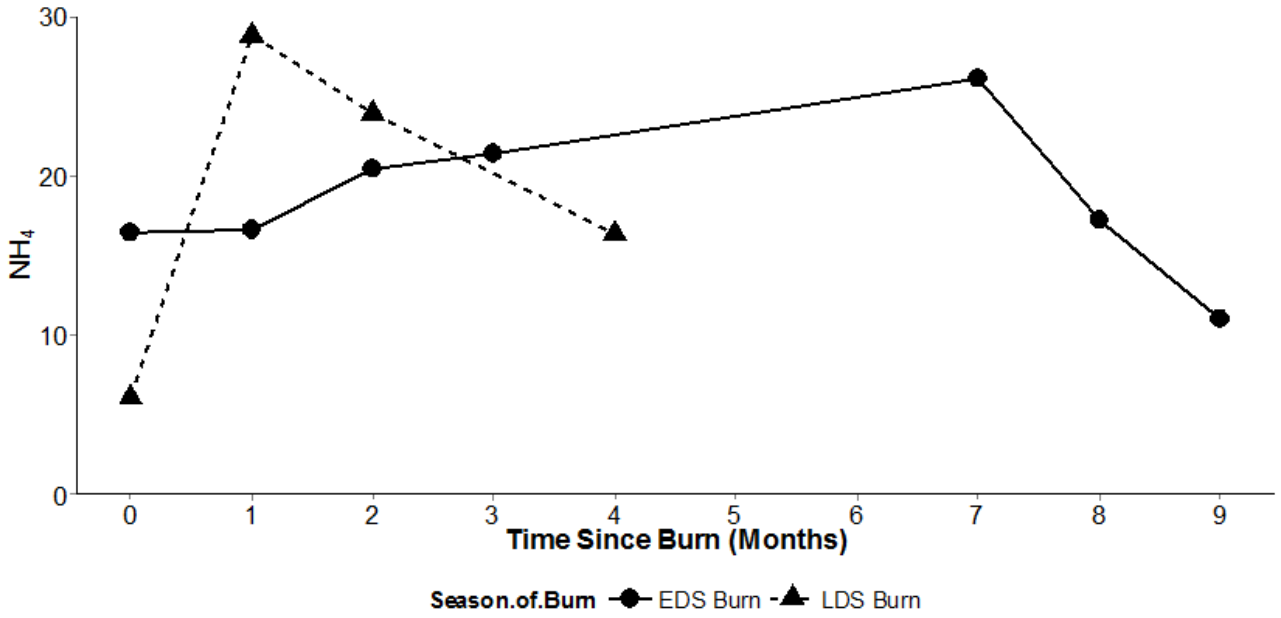

Figure 2.7 Change in grass foliar nitrogen content with time since fire (months) for fires in the early and late dry season. Graph adapted from data from Luhdo (2016).

Other than seasonal fire intensity differences (Govender et al., 2006) and the respective grazing pressure on EDS and LDS burns, the factor that differentiates the length of time that a short grazed patch is maintained between these two seasonal burns is the dormant dry period that the EDS burns “experience”, which the LDS burns do not. Although little growth takes place during the dry season (Tainton, 1999), if the grass is continually being utilised by grazers during this time then it might reduce the stored reserves, making it grow more slowly when the rains do begin. My data do not support this hypothesis. The utilised grass actually grew more quickly once the rains arrived in November than the grass in the exclosure plots which were burned at the same time. The influence of this is perhaps only noticeable through fine-scale assessments of tillering rates, and is possibly best studied over

the long term. Interestingly, both the grazed and ungrazed early burn plots took longer to get going after the rains than the late dry season burn plots – despite being exposed to the same rainfall conditions.

2.5.3. Burn treatment grazer preference

There are few peer reviewed articles that emphasize the role that fire size plays in grazer attraction and more specifically, the ephemeral nature of the fire size effect on forage quantity in differing burn sizes. As already discussed, Allred et al. (2011) showed that grazers spent less and less time in burned areas as time passed after the application of the burns, and this was, regardless of the size of the fire, proportion of area burnt, or the herbivore species. The work by Sensenig et al. (2010) focused on allometric scaling of grazers in resource partition, but noted that dung counts were lowest on their largest fires, and proposed that this was a result of higher quality grass they found on smaller burned areas. This outcome supports my findings, but it is important to note the large fire in their work was far greater (81ha) than my largest burns.

My study relies heavily on the notion that grazers select for burned areas purely because of improved resource quality. However, there is a wide array of work that identifies other reasons as to why ungulates use burned areas. These include top-down (predator avoidance) and bottom-up (forage quality and quantity) processes (Sensenig, et al., 2010; Luhdo, 2016), grazer feeding strategy (Sinclair et al., 2003), timing of reproduction and lambing (Main et al., 1996), and efficiency of foraging (Wilhurst et al., 2000). In a study that ran side-by-side to my own in the Satara landscape, Luhdo (2016) found that forage quality and fear of predation both influenced herbivore use of burned sites, but she also recorded increases in the time spent grazing by Wildebeest, Impala, and Zebra on the burn plots. From the perspective of my study this is the most important point - that grazing levels increase on the plots. From these results and my own work, it is clear that selection for burned areas as a forage resource is a complex process that depends upon several factors.

2.5.4. Problems with my research

As with any research project, there are problems that are discovered, or detrimental events occur that are out of the control of the scientists. My project was no exception to this. Due to the large nature of the landscape level experiment, I found it difficult to balance sample effort and still meet the requirements of sample size for adequate statistical analysis. Sample effort was particular large, and the logistics of collecting all the required data became strained when the need to collect data on both the EDS and LDS burned areas became necessary. This ultimately resulted in the need for sub-sampling at some times during data collection, and resulted in gaps in data as sampling could not be collected on both the EDS and LDS treatments in a single month. Although I believe the data I have collected and used in analysis are adequate, going forward the sample effort may need to be reduced to either allow increased sample size or nullify the need for sub-sampling or data gaps.

My study relied heavily on dung counts as an indication of grazer visitation. Although they have been proven useful in several studies (Archibald et al., 2005; Sensenig et al., 2010; Allred et al., 2011), there are several problems. Some species that defecate in middens, such as white rhinoceros (*Ceratotherium simum*) are less likely to defecate on transects, and the wide array of species that do defecate on transects have different body sizes, dung amounts and sizes. Their differences in dung quantity will therefore not reflect visitation rates perfectly (Archibald et al., 2005; Sensenig et al., 2010). In addition, dung counts may reflect grazer visitation, but do not necessarily indicate that animals are actually grazing. For instance, Luhdo (2016) found that, some species increased grazing activity after the burns. Due to this, the results of my study are arguably inaccurate, although in-field observations indicate that the studied species were visiting the study sites as data indicated. Furthermore, it has been established the important role that mega herbivores have in grazing lawn development and maintenance (Lock, 1972; Currie, 2003; Waldram et. al., 2008; Cromsigt & teBeest, 2014). However, large herbivores were not significant contributors to the maintenance of short grazed patches in my study (pers. obs.). Though the occurrence of white rhinoceros was noted on a few occasions, their presence was low on my plots.. As a result my study can be identified as one that places more emphasis on the role that medium and small bodied ungulates play in

the ecology of short grazed patches. This is arguable more applicable to more protected areas, as mega herbivores are less common than smaller ungulates.

2.5.5. Concluding remarks

The results of this experiment confirm that small fires can attract and concentrate grazers, and that this process acts to keep grass shorter for longer than either fire alone, or no fire. The two objectives of my study were: 1) to investigate how the extent of mammalian herbivore grazing attraction, intensity and duration varies with fire size and season of burn, and 2)to determine the conditions where a fire-grazing interaction can maintain a short-grazed patch for a full growing season.

This study shows that fire and grazing together may contribute to maintaining a short grazed patch, which is pre-cursor requirement for the development of grazing lawns (McNaughton, 1984; Archibald, 2008; Cromsigt & Olff, 2008, Hempson et al., 2014). However, it is evident that this condition is only ephemeral, and at best grass is kept short for no longer than a single season. Regardless, as was hypothesized, the greatest grazer visitation and grazing pressure (shortest grass) was observed on the intermediately sized burns (5ha). Also as hypothesized, EDS treatments exhibited less initial grazer visitation but grass was kept shorter for longer as due to “assistance” by the dormant winter period, and LDS burns had intense grazing but over a much shorter time.

The statistical analysis shows that fire season is more important than fire size. However, the 25ha plot is still a very small fire from an ecological perspective – most fires in savannas are several thousand hectares big (Archibald et al., 2009; Archibald et al., 2010). Therefore all of my fire applications could be considered “small” fires. In terms of season naturally plots were kept shorter for longer with the early season fires, but once the rains came the rates of regrowth were pretty similar on the EDS and LDS plots (Table 2.3). However, grass height at the end of the growing season remained shorter on the LDS plots than on the EDS plots (Figure 2.5) even though the number of animals utilising these plots seemed to be pretty similar.

The work in this chapter shows that fires that are 5ha in size are likely to maintain the highest degree of grazing intensity than smaller and larger fires overall, and that early dry season burns maintain shorter grass for longer, but ultimate that short

grazed patches, a pre-requisite for grazing lawn establishment, cannot be maintained for more than a single season in a savanna landscape. An avenue that I was unable to explore in this experiment was how repeated burns would affect short grazed patch establishment and maintenance. It has been shown that repeated small disturbances over several years can result in grazing lawn development (Cromsigt & Olff, 2008). Furthermore, a factor that this work does not address is that of grass species composition in grazing lawns and its role in grazing lawn development. Repeated small burns which maintain high grazer presence at certain locations in the landscape are likely to alter grass community structure - and could therefore be a mechanism for initiating grazing lawns (Hempson et al., 2014).

In the next chapter, I investigate if repeated, small sized fires can result in a grass community shift from those grasses less associated with grazing lawns, to those more suited to grazing lawn status in the long term. The Experimental Burn Plots (EBP's) in the Kruger National Park represent an opportunity to test this hypothesis. Small fires (7ha – equivalent to our intermediate burn size) have been applied repeatedly for the last 60 years at different frequencies and seasons across various landscapes in the KNP.

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CHAPTER 3: LONG-TERM EFFECTS OF FIRE AND GRAZING ON GRASS COMMUNITY COMPOSITION AND GRAZING LAWN DEVELOPMENT.

3.1. Introduction

3.1.1. Grazing lawn ecology

In African savannas, with their intact indigenous herbivore communities, grazing lawns are recognised as important landscape components that increase biodiversity (Archibald et al., 2005; Cromsigt & Olff, 2008). In his work investigating the effects of hippopotamus (*Hippopotamus amphibius*) grazing in the grasslands of western Uganda, Lock (1972) was the first to conceptualize the development of grazing grass communities that were dependant on grazing activity. However, the term “grazing lawn” was first popularized by McNaughton (1984) when he described it as a community of short grass species that withstands and supports heavy grazing, and provides high nutritional yield per bite. Such lawn grass species are typically short in stature, and stoloniferous or rhizomatous. They can withstand frequent, intense defoliation and maintain a high leaf area index through horizontal growth. In contrast, bunch grass species form dense clumps and are only dominant under little or no grazing. Their tussock-like growth form means they are more easily uprooted by herbivores and cannot maintain sufficient aerial shoots under heavy grazing to become dominant. Many of them will even die out under frequent defoliation (e.g. *Themeda triandra*, Dankwerts, 1984). For grazing lawn persistence, frequent grazing is a necessity to prevent bunch grass species from invading the lawn community (Hempson et al., 2014).

3.1.2. Value and persistence of grazing of lawns

It has been shown that large herbivores can increase the available forage and improve its quality in a landscape and therefore directly benefit from their own grazing activity (Owen-Smith, 1988). Further, most herbivores (apart from bulk grazers) prefer grazing lawn communities over bunch grass-dominated ones (McNaughton, 1984; Arnold, Anderson, & Holdo, 2014; Yoganand & Owen-Smith, 2014). There are several reasons for this. First, grazing lawn species are more easily

digested as a result of lower C:N ratio in the leaves than in the stems (Chaves et al., 2006). Second, they often have greater nitrogen content (which is further promoted by defoliation through up regulation of photosynthesis) (Stock, Bond, Van de Vijver, 2010), and third, they produce more food available per bite, improving the efficiency intake of grazers (due to their greater bulk density) (McNaughton, 1984). In the latter case, if grazing pressure is too great and the sward is reduced too extensively so that sufficient intake is impossible, competition between plants, rather than facilitation, takes place (Arsenault & Owen-Smith, 2008). Similarly, grazing lawns are only thought to be a valuable resource during the growing season (Bonnet et al., 2010). Once rains stop there is no more growth and animals have to find other sources of nutrition. Independent of their role in large herbivore nutrition, grazing lawns represent a novel habitat for numerous birds (Askins et al., 2007; Krook et al., 2007; Augustine and Skagen 2014), insects and invertebrates (Currie, 2003; Van der Plas et al., 2012), and invertebrates (Mgobozi et al., 2008) which are specialised for this short-grass habitat. They are often also associate with different suites of forb and tree species (Cromsigt & teBeest 2014).

Grazing lawns are therefore an important component of biodiversity conservation. However, a key factor in their value is their longevity - an aspect of grazing lawns that has not received enough attention. By investigating the response of established lawn grass patches in the Mountain Zebra National Park of South Africa between 1987 and 2010, Novellie & Gaylard (2013) aimed to investigate the long term persistence of grazing lawns on a small game reserve. The lawn community in question had been favoured by indigenous grazing ungulates that show a selective-habit for short grasses. These included springbok (*Antidorcas marsupialis*), blesbok (*Damiliscus dorcas phillipsi*), and Black wildebeest (*Connochaetes gnou*). When excluding these and all other animals from 1ha lawn patches by means of fencing, Novellie & Gaylard (2013) observed the almost complete replacement of creeping lawn-like grass species by tall bunch grass species over a 20 year period. In contrast, on the unfenced plots, plant species composition remained unchanged over the 20 year period. Furthermore, by monitoring the large stock unit equivalents (ha/LSU) as a proxy for grazing intensity in the last two years of the experiment, Novellie & Gaylard (2013) discovered that the grazing lawns exhibited a far greater carrying capacity (1.8 – 9.7 ha/LSU) than what is considered suitable for commercial

livestock production (14 ha/LSU). Although this work supports that intense grazing promotes the persistence of grazing-tolerant and palatable grass species in place of bunch grass species, Novellie & Gaylard (2013) admit their experiment could not determine the rate of this change. Regardless, this study shows that despite the limited movement of mammalian grazing herbivores in a small game reserve, grazing lawns can be established and further that heavy grazing does not necessarily lead to grass community degradation.

3.1.3. Grazing lawn versus traditional rangeland classification

Traditionally, grasses have been classified purely from an agricultural perspective in terms of their ecological status (as described by Foran et al., 1978), and used for veld condition assessments in rangeland management (Tainton, 1999). This classification is based on individual species reaction to varying intensities of grazing pressure, where the grasses react by either increasing or decreasing in abundance (Foran et al., 1978; Tainton et al., 1980). There are two broad classes into which grasses are classed based on their response, namely; increasers and decreasers. Decreaser species are those that decrease in abundance under heavy utilisation. These species are palatable and thus selected by grazers for forage (e.g. *Themeda triandra*). In contrast, increaser species are those that increase when decreasers decrease. Increaser grasses can be further split into those that increase when under-utilized (Increaser 1, e.g. *Aristida stipitata*), those that increase when they are moderately to heavily grazed (Increaser 2, e.g. *Bothriochloa radicans*), and those that increase when veld is selectively grazed (Increaser 3, e.g. *Elionurus muticus*) (Tainton, 1999; Van Oudtshoorn, 2012).

Although this method of grass classification has been useful for forage management practices, it focuses only on the grazing tolerance and competitive abilities of the grass species – how they respond to grazing or the lack thereof. The palatability of the grasses is not directly considered (Tainton, 1999). Because decreaser species are selected by grazers, they are generally palatable, but this classification does not recognise that palatable species can also be grazing tolerant: i.e. all increaser 2 species are considered undesirable in rangelands, even though many of them (often lawn-grass species) are nutritious and preferred by grazers. Grazing lawns are classified by their physical stature, functional response to grazing, their grazing

value, as well as by their functional role in ecosystems. It is therefore my view that the traditional rangeland method does not account for the value of these productive and grazing tolerant species largely associated with grazing lawns, and thus miss-classifies them. From this it is obvious that the 'ecological status' classification does not encompass the dynamic and complex relationships that need to be understood from an ecological perspective to make accurate conservation management decisions.

3.1.4. Grazing lawn functional types

Although grazing lawns are typically defined by their short stature and ability to withstand heavy grazing, Hempson et al. (2014) describes how distinct types of grazing lawn species can be defined at a growth-form level. They suggest that the main division in grazing lawn types is a grass species' habit to either spread laterally by means of stolons (above the soil surface) or rhizomes (below the surface), or their habit to persist under heavy grazing in a tufted "dwarf form" (caespitose), that does not spread laterally. They further suggest that advanced division of this classification may depend on the stoloniferous type's habit to have stolons either loop over or hug the soil surface tightly, the spacing between stolon nodes, and/or the degree of branching of the stolons. For the purposes of this study, I found the classification stipulated by Hempson et al. (2014) to be overly complicated, and therefore chose to develop my own "grass functional guilds" based on ecological grass status, grazing tolerance, and palatability. I believe this form of classification provides an easy and simpler indication of what grass community changes are taking place, relative to grazing lawns.

It is important to note that not all grazing lawn grasses are palatable and commonly selected by grazers as favourable forage. Some are unpalatable species with low nutrient content, but have been shown to be largely associated with grazing lawns. In other words, some species remain palatable while withstanding heavy grazing, while others do not. Heavy grazing can increase the dominance of two types of grasses – those that avoid grazing by being unpalatable and those that are palatable but tolerate grazing through structural and physiological adaptations. This process is described by Briske (1996) as the grazing resistance concept. The strategy of grazing tolerance includes physiological and morphological mechanisms, whereas

the avoidance strategy can be categorized into spatial and temporal mechanisms, and constitutive mechanisms. In this regard, the type of grass community that dominates under which condition is not yet known.

3.1.5. The role of fire in savanna grass community compositional changes

Most savanna-based fire research has placed emphasis on the influence that short term changes to fire-regimes (specifically fire frequency and intensity) have on the woody component of savannas (Van Wilgen et al., 2003), while there are far fewer published articles investigate the influence of multiple aspects of fire regimes in conjunction with other environmental factors on grass biodiversity, especially in the long-term (Furley et al., 2008).

It is understood that grass biomass (Van Wilgen et al., 2004), fuel moisture content and the weather conditions during burns (Higgins et al., 2000; Govender et al., 2006), all influence fire regimes (fire frequency, season of burn, fire intensity) in savanna systems. Season of burn and fire intensity form a strong association. It has been shown that differences in fire intensity between seasons of burn are primarily a result of differences in the moisture content of available fuel (Govender et al., 2006). Govender et al. (2006) showed that late season burns exhibited the greatest fire intensities due to low fuel moisture at that time of year, regardless of fire frequency. In contrast to this, when fuel moisture was highest (during the growing season), fires exhibited the lowest intensities (Govender et al., 2006). Therefore, one can assume that the response of grass species to fires of differing season is in fact a response to fire intensity (and partly by seasonal differences in rainfall, soil moisture, temperature, etc.). This response will be confounded by increased grazing (Biggs et al., 2003; Smith et al., 2012). However, my results from Chapter 2 suggest that due to the compounding effect of grazing pressure, the dormant dry period, and the timing of the rains, grass is kept shorter for longer on early dry season (EDS, April) burns than on late dry season (LDS, August) burns. This is where EDS and LDS burned areas differ; the EDS burns represents long term grass community change as a result of lower intensity fires, relatively lower grazing pressure, but spending more time in a short grass condition (if grazing imitates that observed on the EDS burns in my landscape experiment, Chapter 2) when compared to LDS burns. It is

evident that the association between fires and grazing, and the resultant affect they have on grass community structure and composition is a complex relationship.

My MSc aims to test whether small repeated fires are able to create this level of persistent grazing, and what the ecological outcome of this is (what sort of grass communities result and what is their ecological value). In Chapter 2 I confirmed what was been established in many other studies (McNaughton, 1984; Guruja & Owen-Smith, 2002; Arsenault & Owen-Smith, 2008; Allred et al., 2011) - that fires attract grazing animals for several months after the fire. Furthermore, I demonstrated that under certain conditions the fire-grazer interaction could keep the grass short until the end of the growing season (i.e. maintain short-grass conditions). The long-term effects of this fire-grazer interaction is therefore likely to be a switch in grass community – to grasses that are more tolerant of heavy grazing. Repeated small burns which maintain high grazer presence at certain locations in the landscape are therefore likely to alter grass community structure - and could therefore be a mechanism for initiating grazing lawns (Hempson et al 2014). The long-term experimental burn plots (EBPs) in the Kruger National Park (KNP) represent an opportunity to test this hypothesis. Small fires (7ha – equivalent to our intermediate burn size in Chapter 2) have been applied repeatedly for the last 60 years at different frequencies and seasons across various landscapes in the KNP.

The effects of these fires on grassland community composition were investigated by Smith et al. (2012). They found the influence of fire on grass community structure to be greatest in higher rainfall sites; where frequent (1-3 year return periods) dry season fires resulted in high grass species richness, evenness and diversity. In contrast, areas of fire exclusion exhibited the lowest of these measures. Overall, they found a varied effect of fire across the climatic and soil fertility gradients, with the effect of fire decreasing in importance with increases in aridity, with herbivory and climatic variability likely having a greater influence on grass community structure and composition (Smith, et al., 2012). Due to sampling methods differing between the pre-treatment and post-treatment surveys of the EBPs, Smith et al. (2012) opted to analyse the two surveys separately – so their results do not necessarily reflect change over time. Moreover, although they do mention that fire-grazer interactions might have influenced the patterns they saw, they were not specifically looking for a grazing effect, nor did they specifically consider change in grazing quality of grasses.

3.2. Aims and predictions

In this chapter I will use the KNP experimental burn plots (EBPs) to test what the long-term consequences of the fire-grazer interaction described in Chapter 2 are for the grass community. In particular I aim to:

i. Determine whether repeated small isolated fires promote grazing-tolerant grass communities through repeatedly concentrating grazing.
ii. If so, determine if fire frequency (Annual and Biennial) or season (early and late dry season) of burn plays a role in the likelihood of grazing lawn development through the fire grazing interaction.

Specifically I predict that pyric-herbivory or the fire- grazing interaction, can initiate a change in grass composition, given sufficient time and regular fire disturbance, from bunch grass dominated systems into grazing tolerant grass systems. The rate and extent of this change will be dependent on the timing and frequency of fires and the resultant grazing pressure on these burnt areas. With regards to frequency, I expect a greater change in grass communities under a shorter (1 year, annual) than a longer fire return period (e.g. 2 year), under similar grazing pressures. Based on results from Chapter 2, I anticipate that there will be greater grazing pressure on recently burnt areas in the late dry season due to the immediate green flush (permitted there is adequate soil moisture) after the winter period when suitable forage has been depleted, and therefore I predict a greater grass species community change in areas that are frequently burnt at this time of the year. I further predict that grasses that are grazing tolerant (e.g. *Urochloa mosambicensis*) will become more prevalent in areas burnt on a regular basis, whereas species that are less grazing tolerant (e.g. *Digitaria eriantha*) will decrease in abundance.

3.3. Methods

3.3.1. Study Area

The Kruger National Park is located in the north-eastern Lowveld region of South Africa (Figure 3.1), in the Mpumalanga and Limpopo provinces (Joubert, 1986; Van Wilgen et al., 1998). At approximately 2 million hectares in size, it is the largest protected area in the country. The park is divided into two climatic zones, north and

south of the Olifants River (Venter et al., 2003). Precipitation decreases from south to north, except for the area of Punda Maria which is found at a higher altitude (Gertenbach, 1980) in the north. The northern arid bushveld zone receives between 300mm and 500mm of rainfall per year, whereas the south and central zone receives 500-700mm per year. The KNP is characterised by hot wet summers and mild, mostly frost-free winters with rainfall concentrated between October and April (Joubert, 1986; Venter et al, 2003). The KNP's geology is complex, but it is roughly divided longitudinally into granitic rocks in the west and basaltic rocks in the east, separated by a thin north-south strip of sedimentary rocks down its centre. As a result, relatively nutrient poor sandy soils and nutrient rich clay soils are found in the west and east, respectively (Joubert, 1986; Gertenbach, 1983; Venter et al., 2003).

The vegetation on the nutrient poor substrates are generally dominated by trees of the Combretaceae (e.g. *Combretum* and *Terminalia* species) and Caesalpinaceae families. Here, unpalatable grasses such as *Pogonarthria squarrosa*, *Aristida* spp., and *Eragrostis* spp. are dominant, yet occur only sparsely. Acacia spp. (Mimosaceae) trees and the nutrient-rich bulk grasses *Themeda triandra*, *Panicum coloratum* and *Urochloa mosambicensis* dominate the nutrient-rich basaltic soils. The herbaceous layer of the park is generally dominated by C4 grass species (Kennedy et al., 2003). Although grazing lawns are a significant component of several southern African parks (Archibald 2005; Cromsigt & Olff, 2008), they generally appear to be confined to sodic sites, termite mounds and hippo grazing areas in Kruger (Gertenbach, 1983; Naiman et al., 2003; Grant & Scholes, 2006).

My experiment took place in the *Sclerocarya birrea*/*Acacia nigrescens* landscape of Satara in the central KNP. This area is located on basaltic soils, and reflects intermediate levels of rainfall (approx. 550mm/ year), relative to the rest of the KNP. The site represents fairly high fertility, moderately low rainfall, and a significant grazer presence and therefore it meets the environmental criteria described by the model created by Archibald et al. (2008) under which we expect grazing lawns to develop.

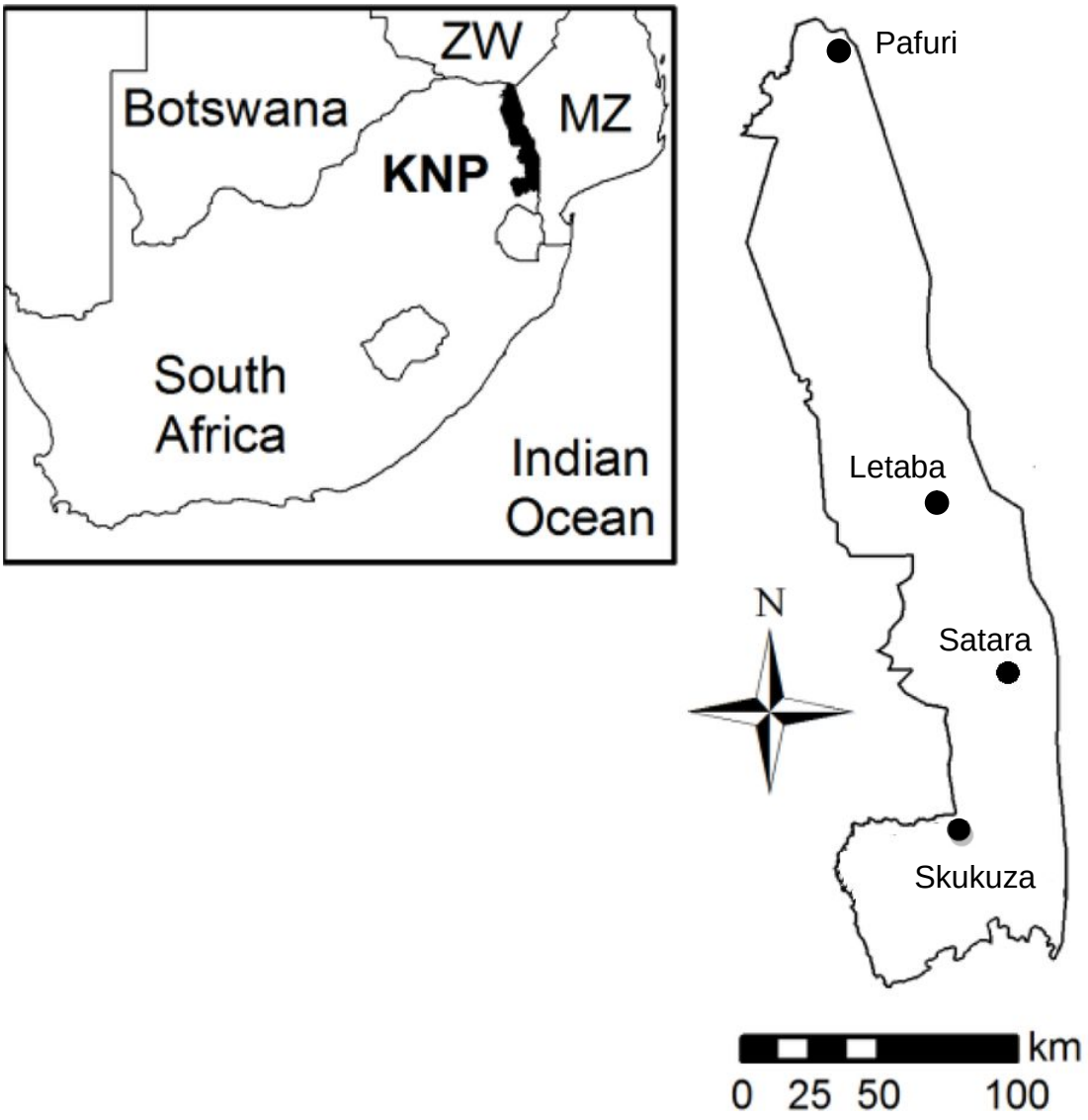

Figure 3.1 Map of the Kruger National Park located in the north-eastern corner of South Africa. Satara is located in the central region of the park (adapted from Colgan et al., 2012).

3.3.2. Experimental burn plots

The experimental burn plot (EBP) trial was established in 1954 to determine the effects of season and frequency of burning in the four major landscapes of the KNP. The experiment included four replicates that were laid out in the following four landscapes of KNP, as described by Gertenbach (1983): the Lowveld Sour Bushveld of Pretoriuskop, the *Combretum*spp/*Terminalia sericea* woodland, the *Sclerocarya birrea*/*Acacia nigrescens* savanna, and the *Colophospermum mopane* shrubland. These landscapes were selected to encompass a broad rainfall gradient and the

major soil types in the park. Consequently, the four sites differ in levels of productivity, woody plant density and levels of herbivory. Within each landscape type, the experiment was replicated four times in the form of strings consisting of 12 – 14 plots, each approximately 7ha in size and subject to different fire treatments that were randomly allocated. Treatments vary in season (early spring, mid and late summer, autumn) and frequency of burn (annual – sexennial). Each string also has a fire exclusion plot. Each plot is separated by a single firebreak, and each string is protected by a double fire break (Van Wilgen et al., 1998; Biggs et al., 2003). Figure 3.3 shows the typical layout of an EBP string. Herbaceous vegetation data has been sampled twice on the EBPs.

The first sampling on the EBPs took place prior to the initiation of the experiment in 1954, and was repeated between in 1998 and 2001. However, the methodology employed during these two phases differed. The pre-treatment survey sampled using a point quadrat technique; a Levy Bridge with 10 metal rods arranged 5cm apart was placed at 6m intervals along diagonal transects in each 7 ha plot, with 1000 points per plot. The number of living rooted plants was recorded for each herbaceous species encountered. The post-treatment survey made use of a step-point method, whereby only 100 points, spaced 2m apart, were sampled along two diagonal transects (total of 200 points). Here, data was expressed as a percentage frequency of each species. This was calculated as 100*(p/t), where p is the number of points encountered for a given species, and t the total number of points sampled (Smith, et al., 2012). To ensure the comparability of data, I resampled my chosen EBP treatments and controls using the same Levy Bridge method as the original survey in 1954. This was done during March and April of 2014. Although information on the 1954 methods is lacking it appears that bare ground and forbs were not included in the initial sampling, so I also excluded them from my 2014 results (i.e. I adjusted my data to proportions which is how the 1954 data were presented). I chose not to use the data collected between 1998 and 2001, as it is believed that as differing methodologies were used, direct comparison between this data is unnattainable (Smith et al., 2012).

I chose to sample three replicates of the EBPs,namely the Satara, N'wanetsi and Marheya replicates (Figure 3.4). These three replicates are found in the *Sclerocarya birrea/Acacia nigrescens* landscape of the Satara region. These replicates were

chosen, as they meet the requirements specified by Archibald et al. (2008) for grazing lawn development. A fourth replicate, Lindanda, which is also found in the Satara region, was ignored due to deviations in its soil characteristics in comparison to the other three replicates (Venter & Govender, 2012; pers. comm. Navashni Govender). This suggests it does not fall under the same landscape, and we assume that data from this site my skew results.

For logistical reasons, I chose to sample only 2 treatments: August annual, April biennial. These treatments allow for seasonal comparison between early and late dry season, as well as between two fire frequencies. I further sampled a new control treatment from outside of the EBP plots. The control (unburnt) plot on the EBPs is not a true control – firstly, it has not been burned for more than 50 years (very unusual in this system) and secondly, due to the close proximity of the original control (unburnt) plots to all other treatment plots, it is likely that they have been exposed to greater than normal grazing pressure. In order to assess the changes on the experimental burns relative to the rest of the landscape I also sampled new control plots outside of the fire experiment for each replicate. These sites will have been exposed to natural burn conditions during the 60 year existence of the EBPs, and therefore reflect “normal” or background conditions of grazing. These control plots were placed in similar soil conditions and landscape position at least two kilometres from the each of the replicate strings to avoid any influence of the EBPs on these plots. Each control plot consisted of an approximate seven ha area, with two diagonal transects in the same fashion as the original methods from 1954. Clearly these new control plots were not sampled in 1954. Although I attempted to ensure that they represented similar conditions to the EBP site it is possible that any ‘change’ in grass composition between 1954 and 2014 on these control sites is not a true change, but rather reflects intrinsic differences between the two sites. Regarding the “new” controls (outside of the EBP’s) and the “old” controls (original unburnt controls started in 1954), my results exhibit both the change between them over a 60 year period, and a the original (1954 unburnt control) and current (new “normal control) differences that exist between the August Annual, April Biennial, and Control treatments.

My study focused on the change in grass community composition on the EBPs between 1954 and 2014. I assessed this in various different ways. Firstly I ran an

ordination to test for a change in species composition. To explore the ecological implications of these changes I classified the grass species present using both the ecological status (increaser/decreaser) classification of Foran et al (1978) and a more general functional guild classification (tussock, stoloniferous, disturbed) from Van Oudtshoorn (2012). I also selected six key grass species whose ecology and response to fire/grazing are well understood. I wanted to sample species across the full spectrum of grazing tolerance and palatability so I chose species that are known to be palatable/unpalatable and known to be grazing tolerant/grazing intolerant (Figure 3.5). By selecting a few key species that are at least certain representatives of these communities, we can produce a relatively clear expectation of changes through looking at their individual changes. Here, it is important to note that grass species exhibit extensive regional variability in their structural and functional ecology, assumedly as a result of ongoing adaptions to differing environmental factors (Hempson et al., 2014). For this reason, it is difficult to maintain a species-specific functional type classification (Hempson et al., 2014). The full list of species encountered on the EBPs in this research, including their ecological status and functional guild classification, are included in Appendix 1 of this chapter.

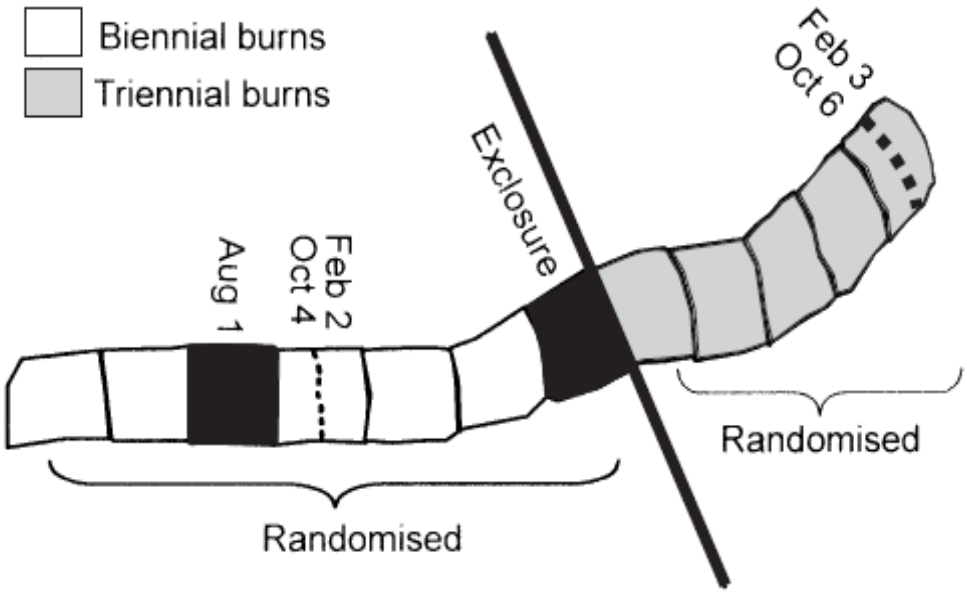

Figure 3.2 A diagram of an experimental burn plot string. Each replicate consists of two sections of plots. The first section is made up of a fire exclusion plot, August annual and five biennial treatments. The second consists of the five triennial treatments. Four and six year treatments where created at the *Mopane* and *Sclerocarya birrea*/*Acacia nigrescens* replicates by dividing the February biennial and triennial treatments, respectively (Biggs et al., 2003)

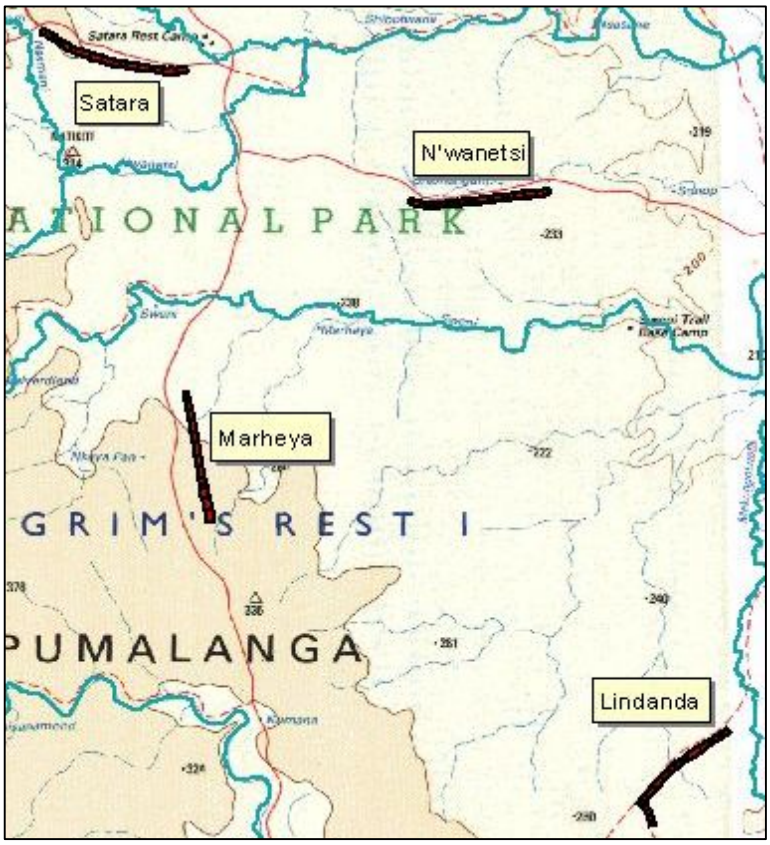

Figure 3.3 The location of the four Experimental Burn Plot strings found within the *Sclerocarya birrea/Acacia nigrescens* landscape of Satara in the Kruger National Park, South Africa

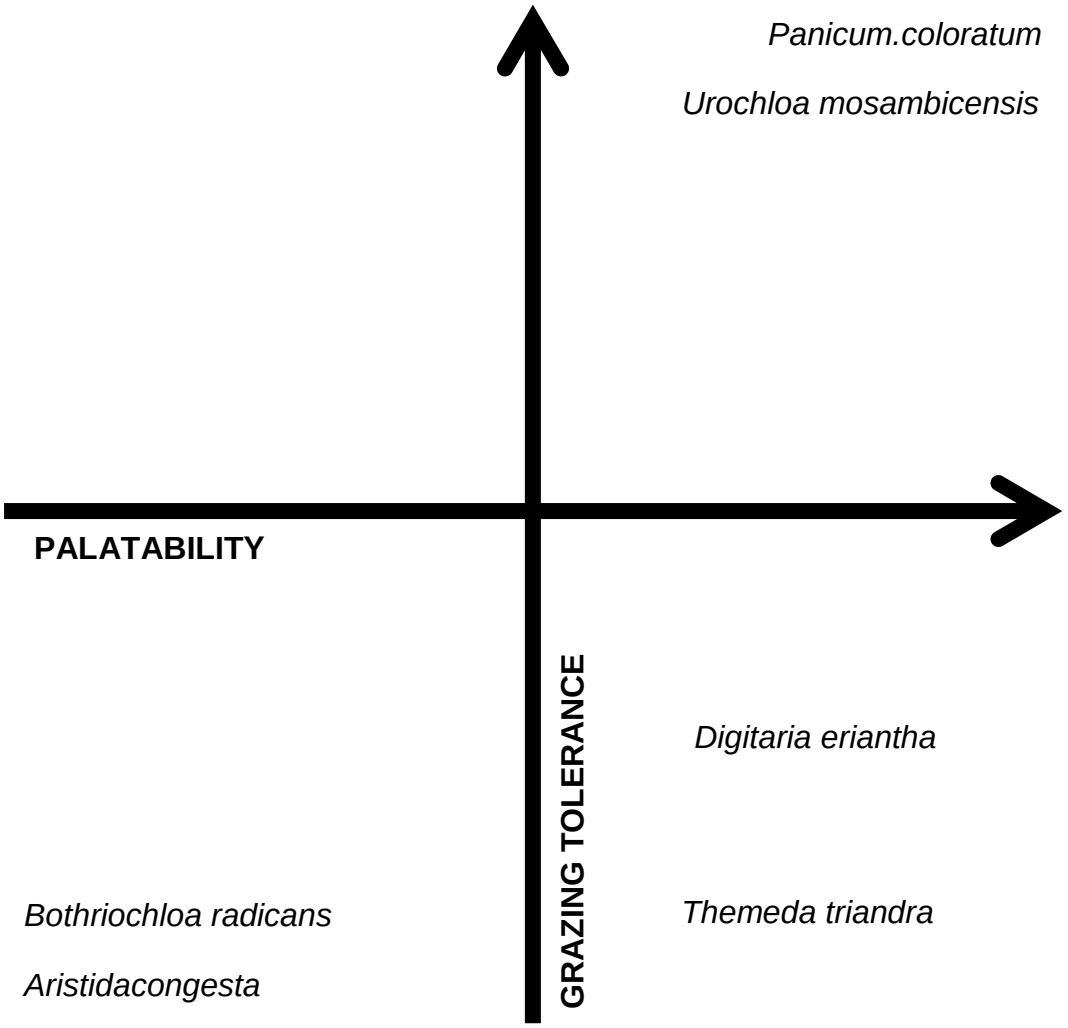

Figure 3.4 Locations of the six key species on axes of palatability and grazing tolerance. If small frequent fires promote grazing lawns then we would expect an increase in the grazing tolerant and palatable grasses. If they attract grazers but do not promote grazing lawns we expect an increase in the grazing intolerant and unpalatable grasses as well. Finally, if frequent small fires do not attract grazers then we do not expect a decrease in the grazing intolerant and palatable grasses. We could not identify any grasses that were both grazing tolerant and unpalatable so this part of the axes space is not populated.

3.3.3. Data analysis

All data analysis was conducted using the R open source statistical software (Version 3.2.1). All statistically comparable groups were tested for normality using the Shapiro-Wilks test.

3.3.3.1. Historical KNP data

As explained in the introductory section, it is known that changes in grazer numbers, rainfall, or the size and number of fires taking place in a landscape can influence the establishment of grazing lawns. I made use of the Pearson's correlation test on historical data of the KNP in order to rule out the possibility that changes in any of these variables during the existence of the EBP experiment may influence grazing lawns establishing. By plotting time (year) against annual rainfall (mm), area burned (hectares), and the estimated number of grazers in the Satara region over the last 60 years, I can determine if there is any evidence to suggest that long term changes have taken place. Animal estimates (Impala, Warthog, Waterbuck, Blue wildebeest and Burchells' Zebra only) of the entire Park were used, as regional data was not available for Satara alone. These species reflect the more common species found in the study area. Records for other species – such as elephant, buffalo and more rare species (Tsessebe etc.) were incomplete and therefore removed from the analysis.

3.3.3.2. Uniformity of EBP species composition

In order to determine the overall significance of changes occurring on the EBPs, I made use of a non-metric multi-dimensional scaling ordination (NMDS) to show similarity of grass species composition (based on average frequency per species) between replicates and treatments on both the 1954 and 2014 data, respectively. By determining the uniformity, or similarity of grass species composition, between replicates and treatments in both 1954 and 2014, I can determine whether a difference between replicates or treatments existed prior to the initiation of the EBP experiments, which could suggest that environmental factors were already altering grass species composition.

Ordination is a multivariate exploratory data analysis technique used to visualize the level of similarity between groups within datasets (Legendre & Legendre, 1998). After comparing the robustness of several ordination techniques on simulated data, Minchin (1987) came to the conclusion that non-metric multidimensional scaling ordination, specifically when using the Bray-Curtis dissimilarity coefficient, is a far more robust and accurate ordination technique than any other, and suggested that it should see far more use by community ecologists. At the time of his article, very few ecologists made use of this technique (Minchin, 1987). The NMDS algorithm

determines the similarity of groups based on the distances between and among samples of a data matrix. The calculated distances are regressed against the original data matrix, from which estimated ordination distances are calculated for each sample pair. The goodness of fit, or “stress”, of the regression is calculated as the sum of squared differences between the predicted distances of the regression, and the calculated ordination distances. Stress is dependent on the number of samples, as well as on how many variables are present (Legendre & Legendre, 1998). The most common stress calculation is that of Kruskal’s stress formula:

$$Stress = \sqrt{\frac{\sum_{h,i}(d_{hi} - D_{hi})^2}{\sum_{h,i} D^2{}_{hi}}}$$

Here, d_{hi} represents the calculated ordinated distance between two samples (*h* and *i*), and $D_{hi}$is the regression predicted distance. The Kruskal’s stress test is run several times, making minor adjustments to the position of samples in the ordination space. The entire NMDS process is repeated until the lowest possible calculated stress is achieved. The stress values provide an indication of how well the ordination represents the distances among samples (Legendre & Legendre, 1998). There are several rules of thumb that appear to exist for interpreting stress values. However, it appears that most are based on personal experience (pers. obs.), and I have found no peer reviewed articles discussing the matter. Ultimately, low stress generally indicates that the ordination is a good representation of the distances among samples, whereas high stress values show the opposite. The methods and suggestions made by Minchin (1987) are incorporated into the *vegan* R package. I made use of the *metaMDS* function, and the average difference in frequency between 1954 and 2014 for each species was used as an indication of changes in abundance of each grass species.

3.3.3.3. Determining which grass species showed similar change

A method of cluster analysis, namely the Partitioning Around Medoids (PAM) algorithm (*cluster* R package), was used in order to identify groups of grass species that exhibit similar levels of change in frequency between 1954 and 2014, for each treatment sampled on the EBPs. This provides an indication of which species exhibit similar reactions (changes in frequency) to each of the different fire treatments (April

biennial, August annual, and Control). For this analysis I used the difference in frequency between 1954 and 2014 as my input data as an indication of the amount of change that took place. The PAM method is a partitioning method of cluster analyses developed by Kaufmann and Rouseeuw (1990) who state that “the main aim of partitioning objects into a number of clusters is to find in such a way that objects in the same cluster are as similar as possible and objects in different clusters are as dissimilar as possible”. The PAM algorithm is based on mediods: representative objects of the datasets with the lowest mean dissimilarity to other points in the dataset (Elavaras, 2011). The PAM process is identical to that of the more popular k-means algorithm (developed by MacQueen, 1967), yet the use of mediods rather than means makes it a more robust method. A disadvantage to the use of the PAM algorithm is that it the number of clusters must be stipulated in its calculation (Shraddha & Emmanuel, 2014). This is not particularly conducive to accurately identifying clusters in ecological data, and therefore I also made use of the *pvclust* function (*pvclust* R package) to identify and determine the statistical significance of clusters in the data. This method provides a bootstrap probability (BP) value and approximately unbiased (AU) p-value for each cluster. This is useful for my analyses, as it will show which grass species respond similarly and dissimilarly to different fire and grazing on the EBPs

Cluster dendrograms were plotted of all grass species in each treatment showing the similarity of grass species change. Dendrograms are presented as phylograms for ease of interpretation.

3.3.3.4. Exploring change in grass communities over time

In order to determine if significant change has taken place towards a grazing lawn like community, I studied the difference in abundance between 1954 and 2014 of the six key grass species of known grazing tolerance and palatability that occurred in the study sites (*P. coloratum*, *U. mosambicensis*, *B. radicans, A. congesta, D. eriantha*, and *T. triandra*), the ecological status classes (Increaser 2 and Decreaser), and the functional guilds (Tussock, Stoloniferous, and Disturbed). For this analysis, I calculated the difference in frequency between 1954 and 2014 for each grass species on the EBPs. To determine if species or groups saw significant absolute change, I conducted a one-sample t-test on parametric data, and non-parametric

equal Wilcoxon signed rank test used for non-normally distributed data. Results are presented using boxplots (change in frequency), exhibiting the median, maximum and minimum or data for each group; however the mean and standard error are reported in text.

3.4. Results

3.4.1. Historical data – Kruger National Park

Over the period during which the EBPs have been maintained there is no clear trend in total area burned (t = -0.993, df = 48, p-value = 0.326, r = -0.142) or rainfall (t = -0.056, df = 55, p-value = 0.955, r = -0.008) in the Satara region of the Kruger National Park (Figure 3.6). There is an obvious oscillating trend that correlates between the two – as would be expected (Van Wilgen, 2004).Park-wide grazer numbers have varied significantly over the time period, but again without any clear trend (t = -1.569, df = 36, p-value = 0.125, r = -0.253). The sudden increase in grazer numbers observed in early 2000 is probably due to changes in sampling methods (pers. comm. Sam Ferreira).

3.4.2. Uniformity of experimental burn plots

Grass community composition between replicates differed in 1954 (R^2 = 0.722, p = 0.017), but were similar in 2014 (R^2 = 0.135, p = 0.849) (Figure 3.7). However, when exploring the data at treatment level (Figure 3.8), we observe no difference in species composition in both 1954 (R^2= 0.120, p 0.746) and 2014 (R^2 = 0.399, p = 0.082). This is a slightly confounding result, as at the replicate level data suggests that the Satara landscape was heterogeneous in terms of species composition prior to the initiation of the EBPs, whereas at the treatment level, we observe the opposite indication. This could be explained by the small sample sizes made available by the nature of the experiment. However, both the 1954 (stress = 0.032) and 2014 (stress = 0.043) ordinations exhibit low stress levels, and can be assumed to represent the differences in data well. Regardless, by observing the ordination plots one could make a conservative assumption that a grass species composition change has at least occurred between 1954 and 2014, suggesting that fire and grazing does play some role in grass community compositional change.

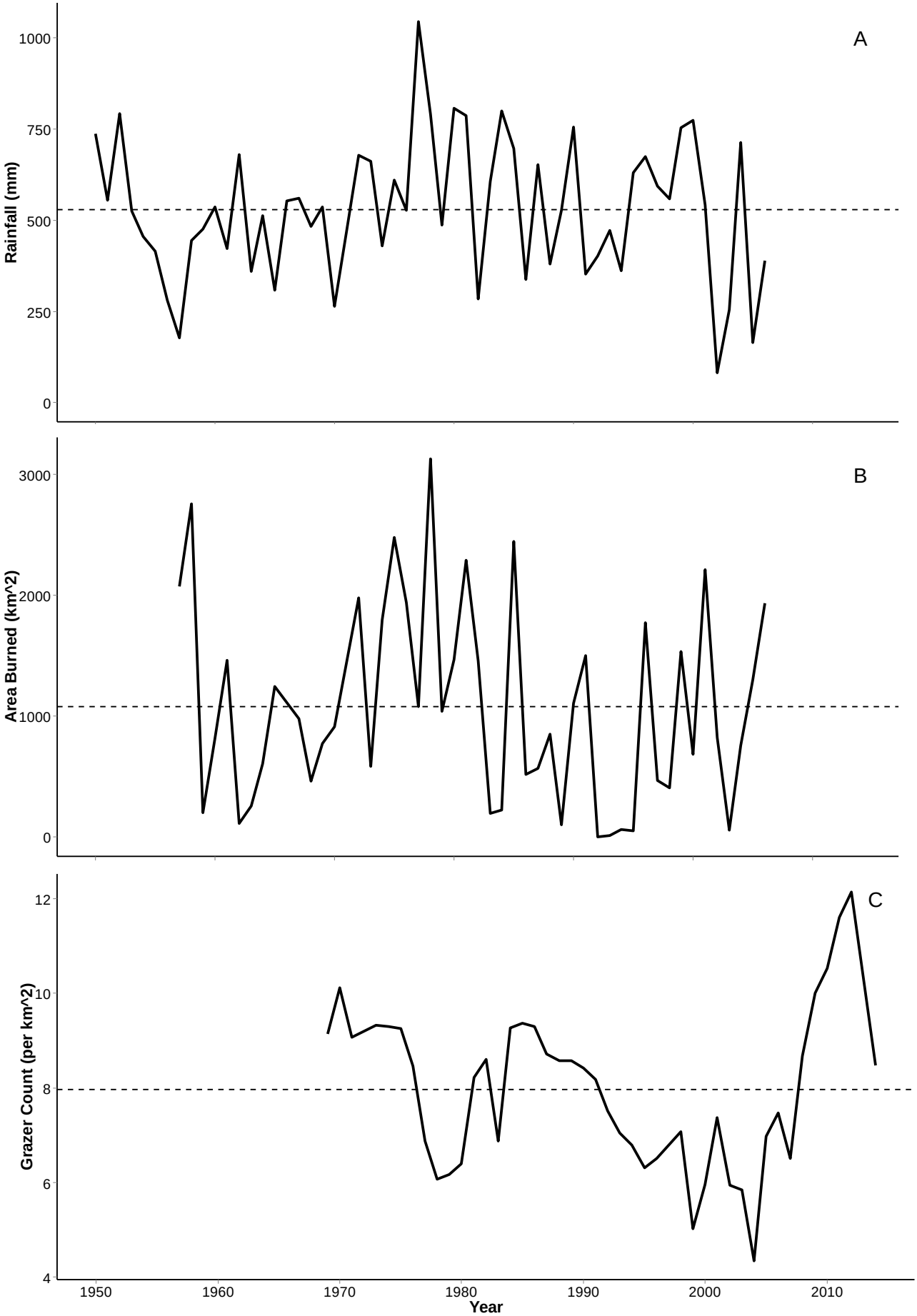

Figure 3.5 The change in rainfall (mm, A) and fire (area burnt, B) in the central region (Satara) of the Kruger National Park from the 1950s to 2006. The change in the number of grazers per square kilometre for the entire Park is also depicted (1969 – 2014, C). The dotted lines indicate the mean for the respective variables over the time period.

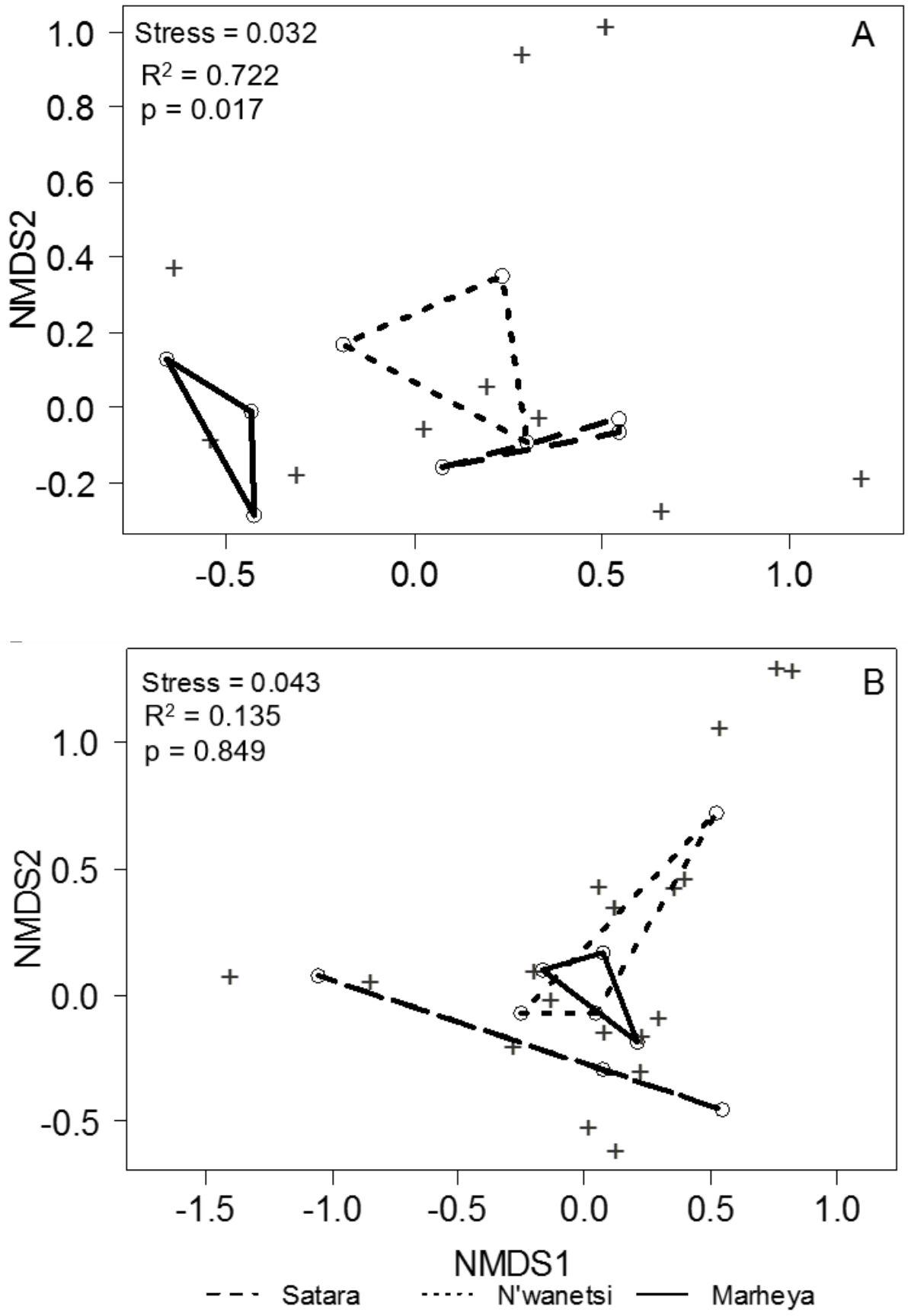

Figure 3.6 Non-metric multidimensional scaling ordination plot of species composition similarity between three replicates (Satara, Marheya, N'wanetsi) of the EBPs in 1954 (A) and 2014 (B).

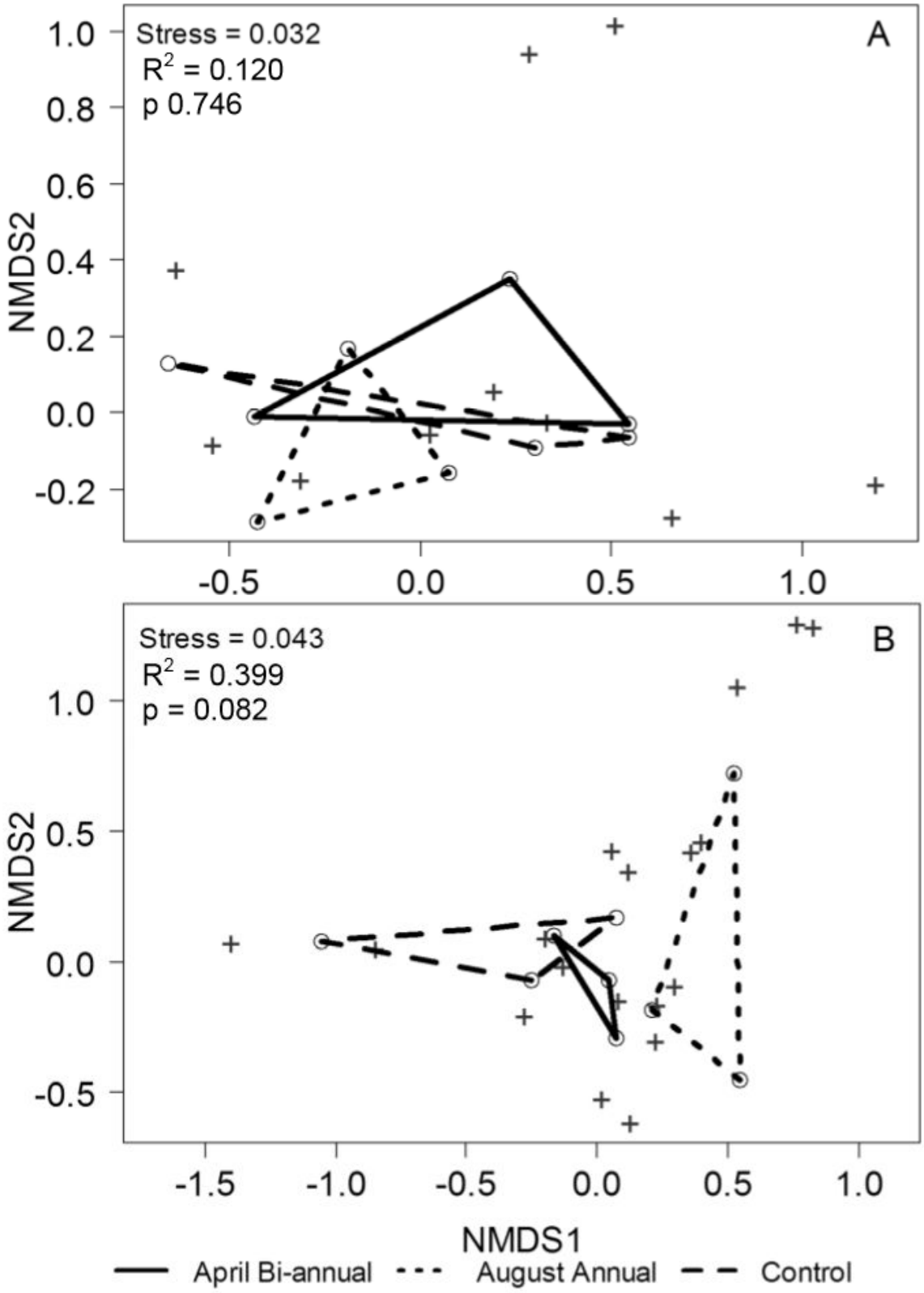

Figure 3.7 Non-metric multidimensional scaling ordination plot of species composition similarity between three treatments (April biennial, August Annual, and Control) of the EBPs in 1954 (A) and 2014 (B).

3.4.3. Comparing change in grass species composition between treatments

Three distinct clusters are evident in the grass community found on the April biennial treatment plots of the EBP in Satara (Figure 3.9). A large cluster (A) exhibiting only minor change over the 60 year period (m = 0.931 ± 0.551 SE) is represented mostly by those species mostly found in disturbed environments, but still exhibits a diverse ecology. A notable outlying member of this cluster is *U. mosambicensis* (Increaser 2, Stoloniferous, m = 12.002 ± 2.783 SE), which exhibits a relatively large increase in comparison to the other species. Interestingly, another stoloniferous species, *P. coloratum* is classified in its own cluster exhibits the greatest increase in abundance since 1954 (Decreaser, Stoloniferous, m = 27.147 ± 2.522 SE). Species exhibiting large decreases (B), *B. radicans* (Decreaser, Tussock, m = -25.045 ± 6.639 SE) and *D. eriantha* (Decreaser, Tussock, m = -17.923 ± 7.085 SE) are grouped together.

On the August annual treatment (Figure 3.9), a cluster mostly dominated by Increaser 2 grass species is prominent (A), which also exhibits only minor change since the initiation of the experiment (m = 1.496 ± 0.421 SE). Other than this cluster, five other species represent their own distinct groups, showing dissimilarity from all other species. These are; *D. eriantha* (m = -27.947 ± 5.289 SE), *T. triandra* (Decreaser, Tussock, m = -10.382 ± 5.212 SE), *B. radicans* (m = -3.996 ± 13.067 SE), *P. coloratum* (m = 4.192 ± 7.148 SE), and *U. mosambicensis* (m = 23.209 ± 10.315 SE). Of these species, all those that saw a decrease in abundance are considered tussock species, while like on the April biennial treatment both the stoloniferous species saw increases.

On the Control treatment (Figure 3.10), *B. radicans* (m = -40.830 ± 15.879 SE), *D. eriantha* (m = -10.732 ± 12.868 SE), and *T. triandra* (m = 17.117 ± 12.134 SE) once again represent their own single-species clusters, each of which are considered tussock growth forms. As was found on the April biennial and August annual treatments, the largest cluster on the Control plots (A) consisted largely of pioneer or sub-climax grasses associated with disturbed areas. This cluster has also exhibited only minor changes (m = 1.134 ± 0.397 SE).

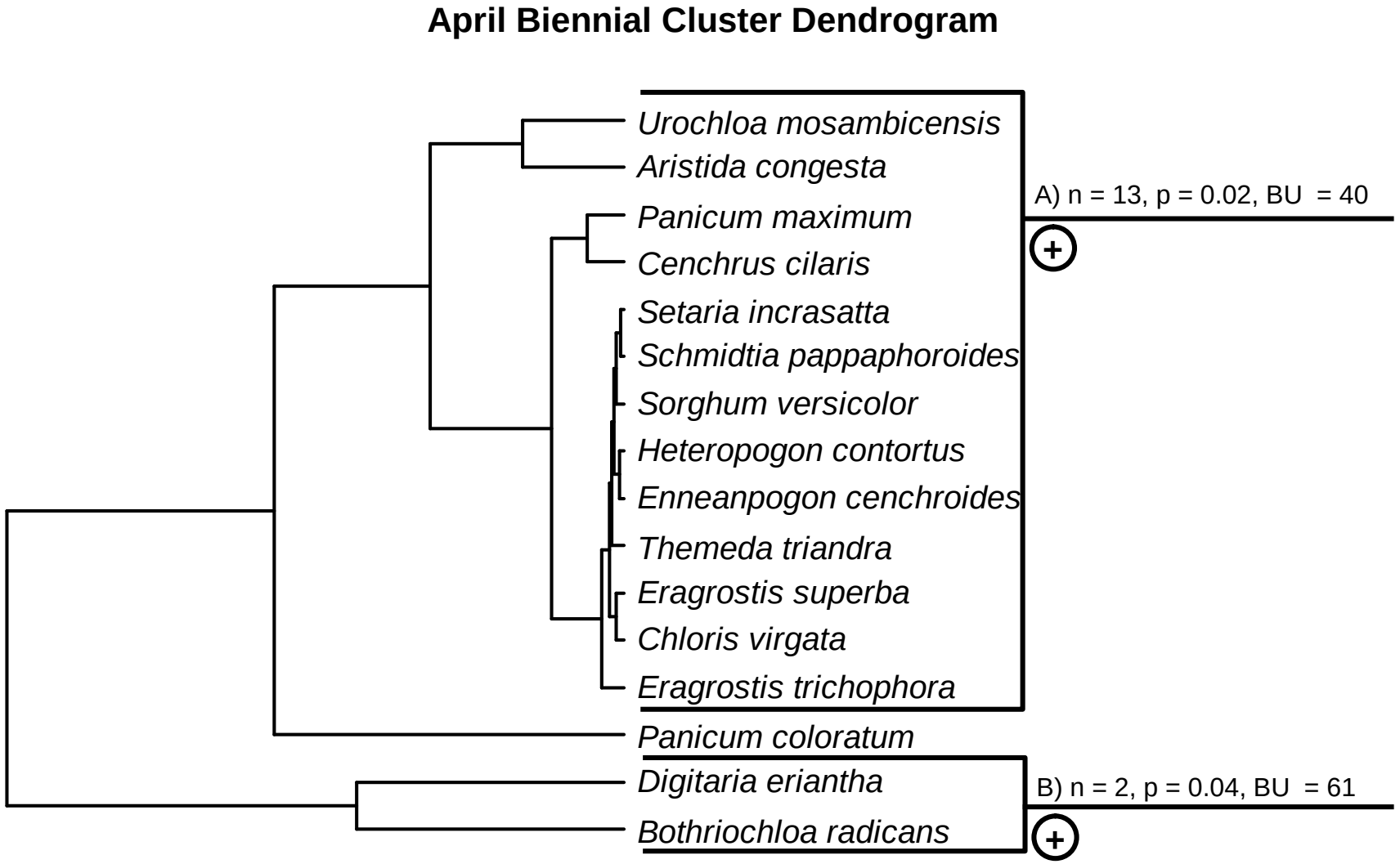

Figure 3.8 Cluster dendrogram illustrating clusters of grass species exhibiting similar changes in frequency between 1954 and 2014 on the April-biannual treatment of the Experimental Burn Plots in the Satara Region of the Kruger National Park. Individual clusters are shown with their associated cluster size (n), approximate unbiased significance value (p), and bootstrap probability value (BU). Species that do not represent a similar change to a distinct cluster remain unmarked. Positive and negative symbols indicate if the average change within clusters is increasing or decreasing, respectively.

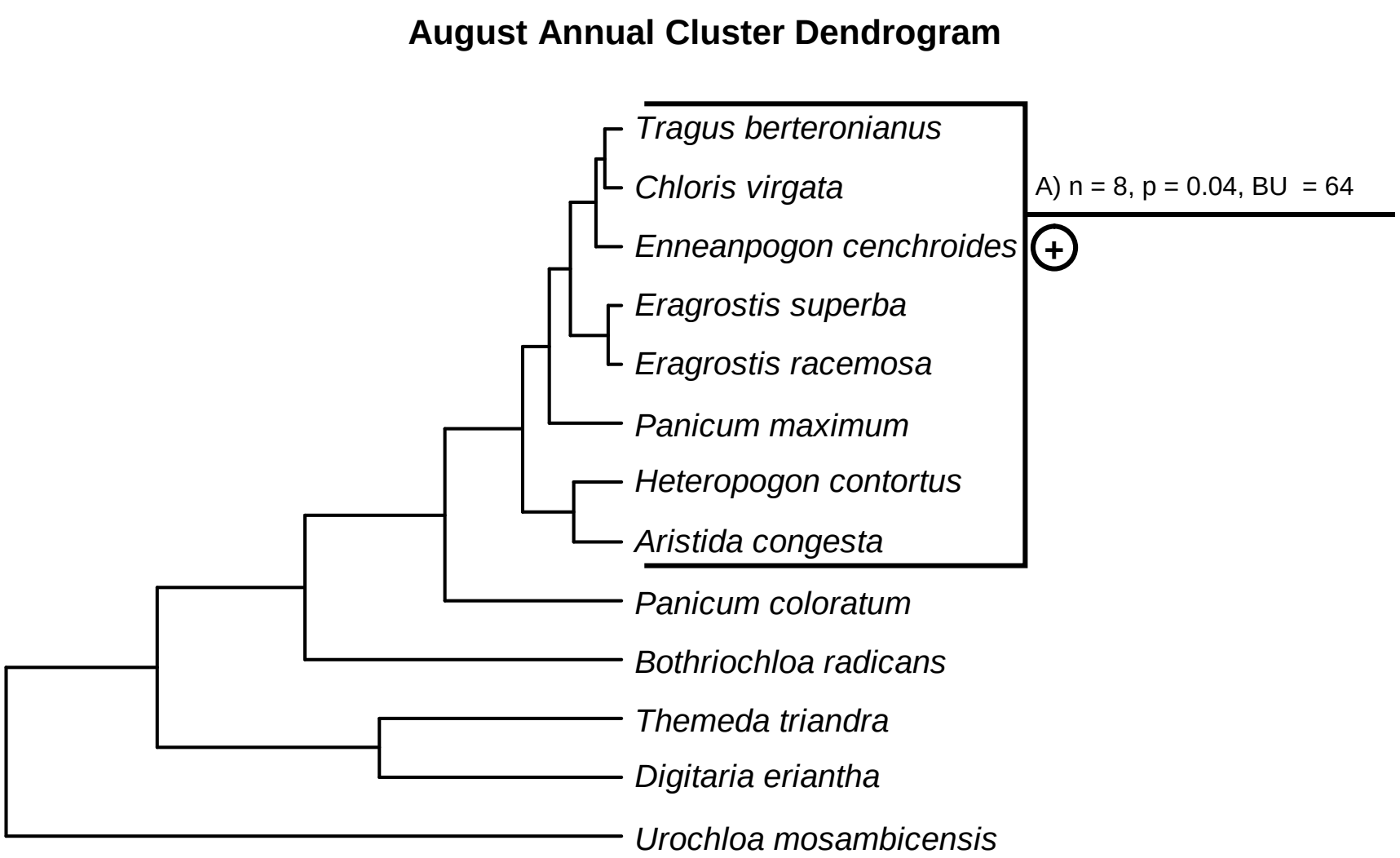

Figure 3.9 Cluster dendrogram illustrating clusters of grass species exhibiting similar changes in frequency between 1954 and 2014 on the August Annual treatment of the Experimental Burn Plots in the Satara Region of the Kruger National Park. Individual clusters are shown with their associated cluster size (n), approximate unbiased significance value (p), and bootstrap probability value (BU). Species that do not represent a similar change to a distinct cluster remain unmarked. Positive and negative symbols indicate if the average change within clusters is increasing or decreasing, respectively.

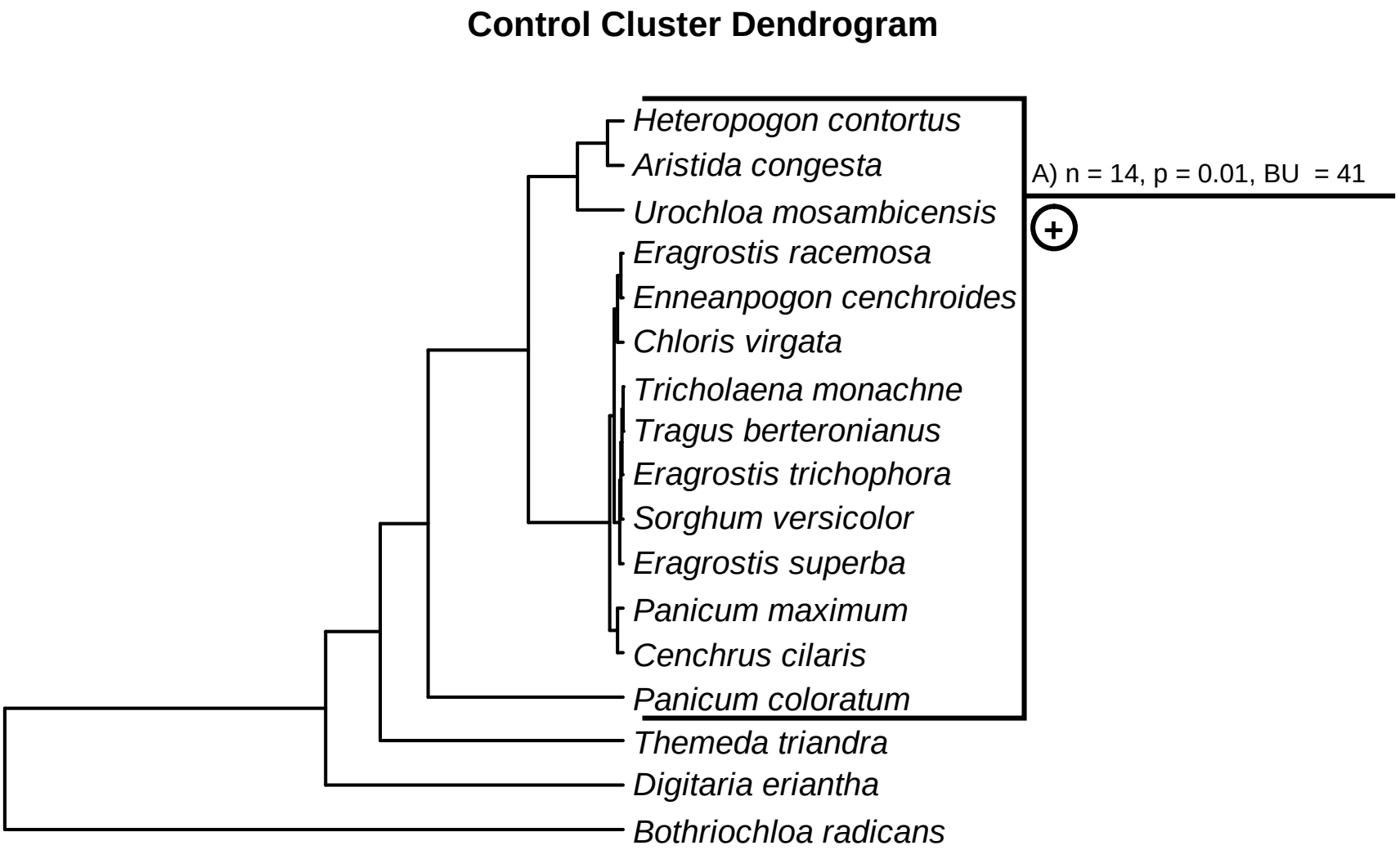

Figure 3.10 Cluster dendrogram illustrating clusters of grass species exhibiting similar changes in frequency between 1954 and 2014 on the Control treatment of the Experimental Burn Plots in the Satara Region of the Kruger National Park. Individual clusters are shown with their associated cluster size (n), approximate unbiased significance value (p), and bootstrap probability value (BU). Species that do not represent a similar change to a distinct cluster remain unmarked. Positive and negative symbols indicate if the average change within clusters is increasing or decreasing, respectively.

3.4.4. The effect of treatment on grass species, ecological status and guild.

Analyses of the treatment effect (Figure 3.12) showed mostly statistically insignificant results, however the general outcomes allow for interesting deductions. *Bothriochloa radicans* shows a substantial decrease in abundance on the Control treatments (m = -40.830 ± 15.879 SE), yet does not change on the August annual treatments (m = -3.996 ± 13.067 SE). *Digitaria eriantha,* which shows a contrasting result to that of *B. radicans*, with a significant decrease observed on the August annual treatment (m = -27.947 ± 5.289 SE) and only a relatively small decrease on the Control (m = -10.732 ± 12.868 SE). Of the remaining key species, *U. mosambicensis* saw an increase on the April biennial treatment, yet also increased on the other treatments. As noted earlier, the other stoloniferous species (*P. coloratum*) also observed an increase on the April biennial treatment (m = 27.146 ± 2.522 SE), yet also saw a similar increase on the Control (m = 16.722 ± 8.867 SE). *Aristida congesta* exhibits an increase in abundance on all three treatments, yet only significantly so on the August annual (m = 6.385 ± 0.996 SE, p = 0.022) treatment. Finally, *T. triandra* (Tussock, Decreaser) displayed distinct difference in reaction between the three treatments, although all changes were statistically insignificant (p > 0.05). *Themeda triandra* saw almost no change on the April biennial treatment (m = 1.064 ± 0.264 SE), a decline on the August annual plots (m = -10.382 ± 5.212 SE), and a substantial increase on the Control (m = 17.117 ± 12.134 SE).

With respect to the ecological grass status (Figure 3.12 B), Decreaser and Increaser 2 grasses exhibit contrasting changes on each of the three replicates. As would be expected in areas of increased grazing pressure, as is believed to be the case on the EBPs (Biggs et al., 2003), on the August annual treatment Decreasers saw a substantial decrease (m = -9.053 ± 4.340 SE, p = 0.003), while Increasers amplified significantly (m = 5.432 ± 3.109 SE. This response has resulted in the August annual treatment now being dominated by Increaser 2 species (Figure 3.13). Regarding the functional grass guilds (Figure 3.12 C and Figure 3.14), stoloniferous and tussock grasses exhibit an increase and decrease across all treatments of the EBPs respectively. Stoloniferous grasses saw their greatest increase on the April biennial treatments (m = 19.575 ± 3.617 SE), while tussocks experience their greatest decrease (m = -9.029 ± 6.451 SE).

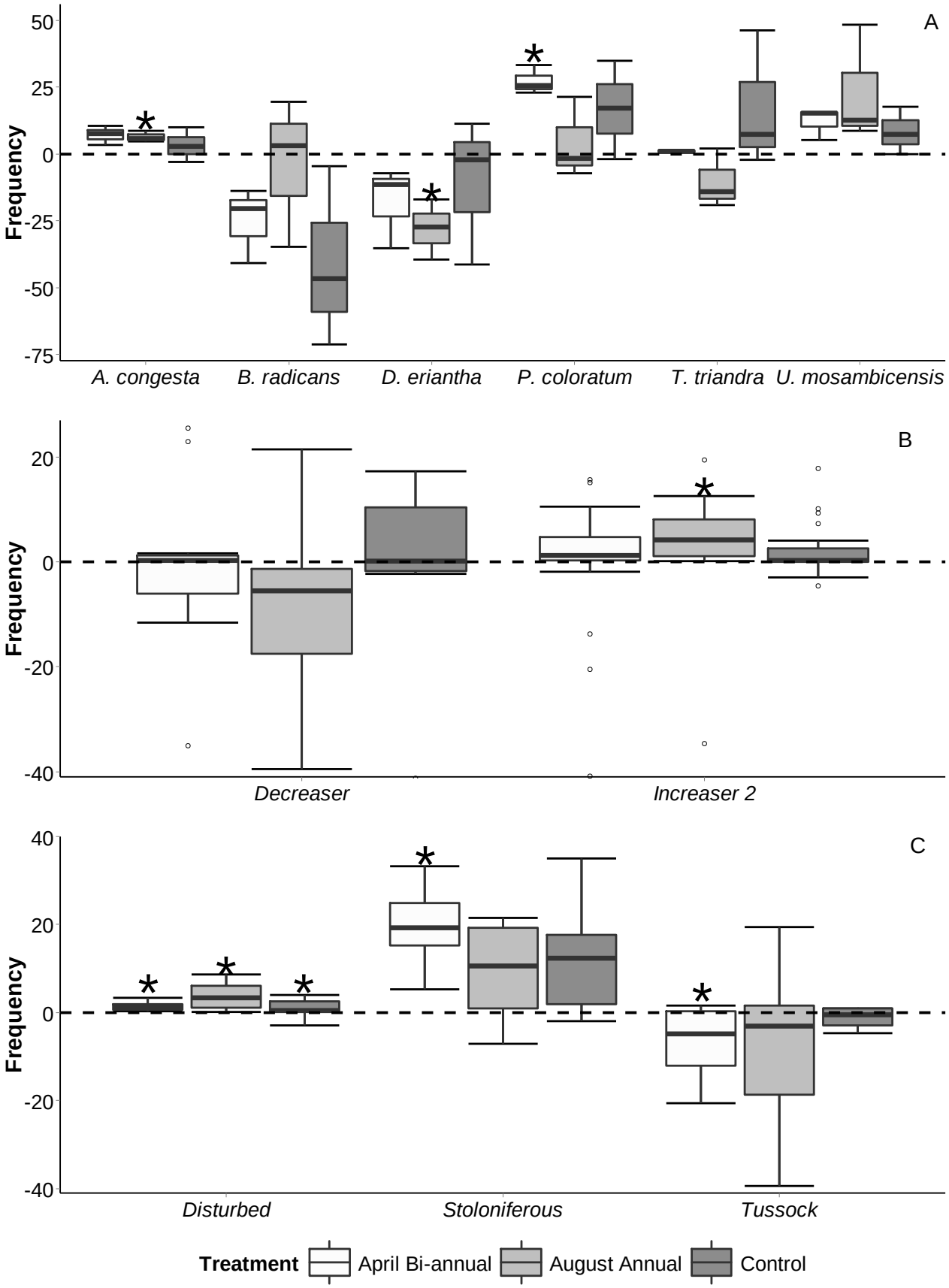

Figure 3.11 The average difference in frequency between 1954 and 2014 of six key grass species (A), the ecological status grass groups (B), and grass guilds (C) between three treatments of the Experimental Burn Plots (April Biennial, August Annual and Control). An asterix above a species group indicate a group where change is significantly different from zero ($p < 0.05$), indicating a significant change.

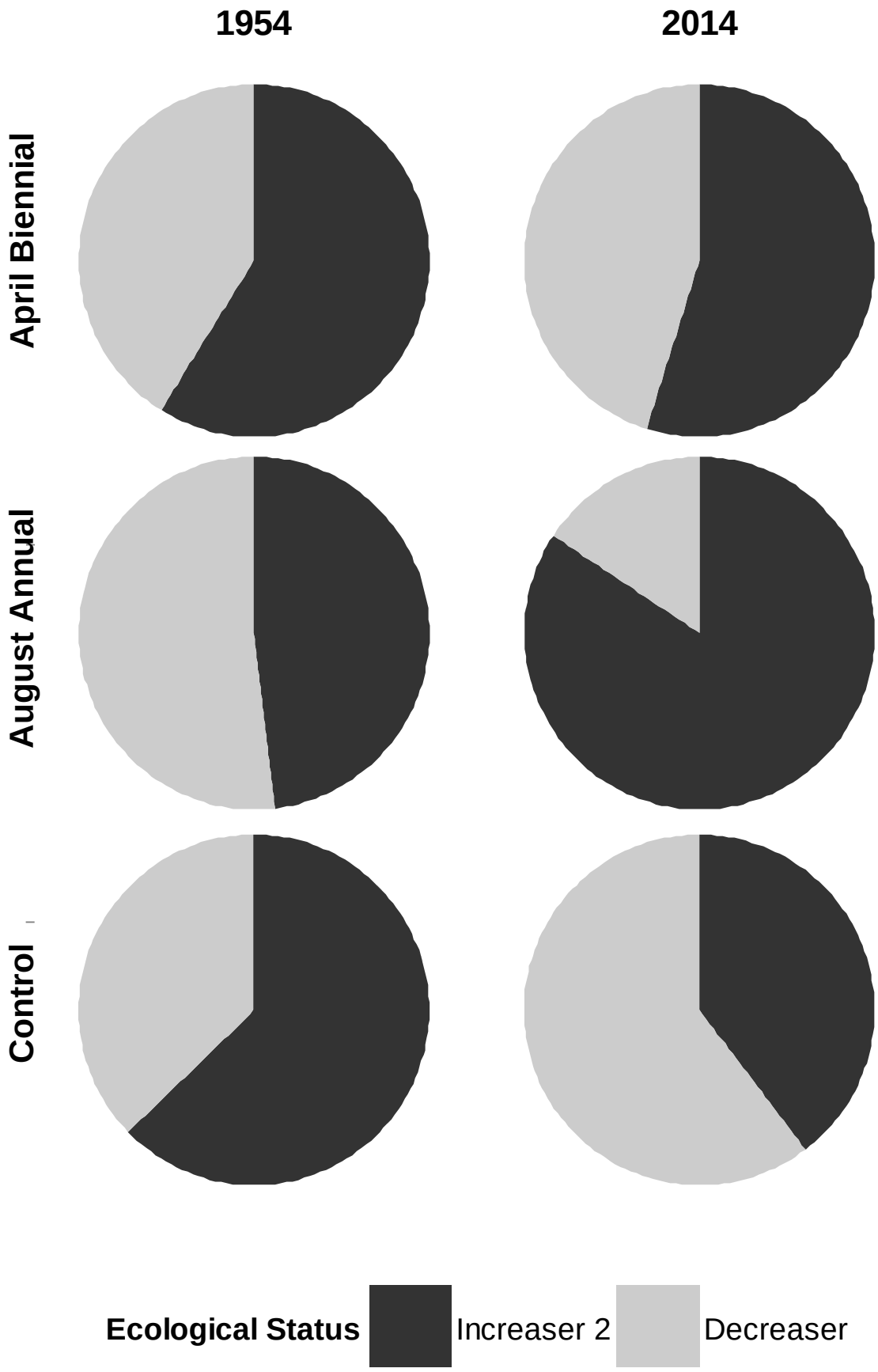

Figure 3.12 Pie charts illustrating percentage composition of ecological grass status classes on the April biennial, August annual, and Control treatments in 1954 and 2014 of the EBP's in the Satara region of the Kruger National Park.

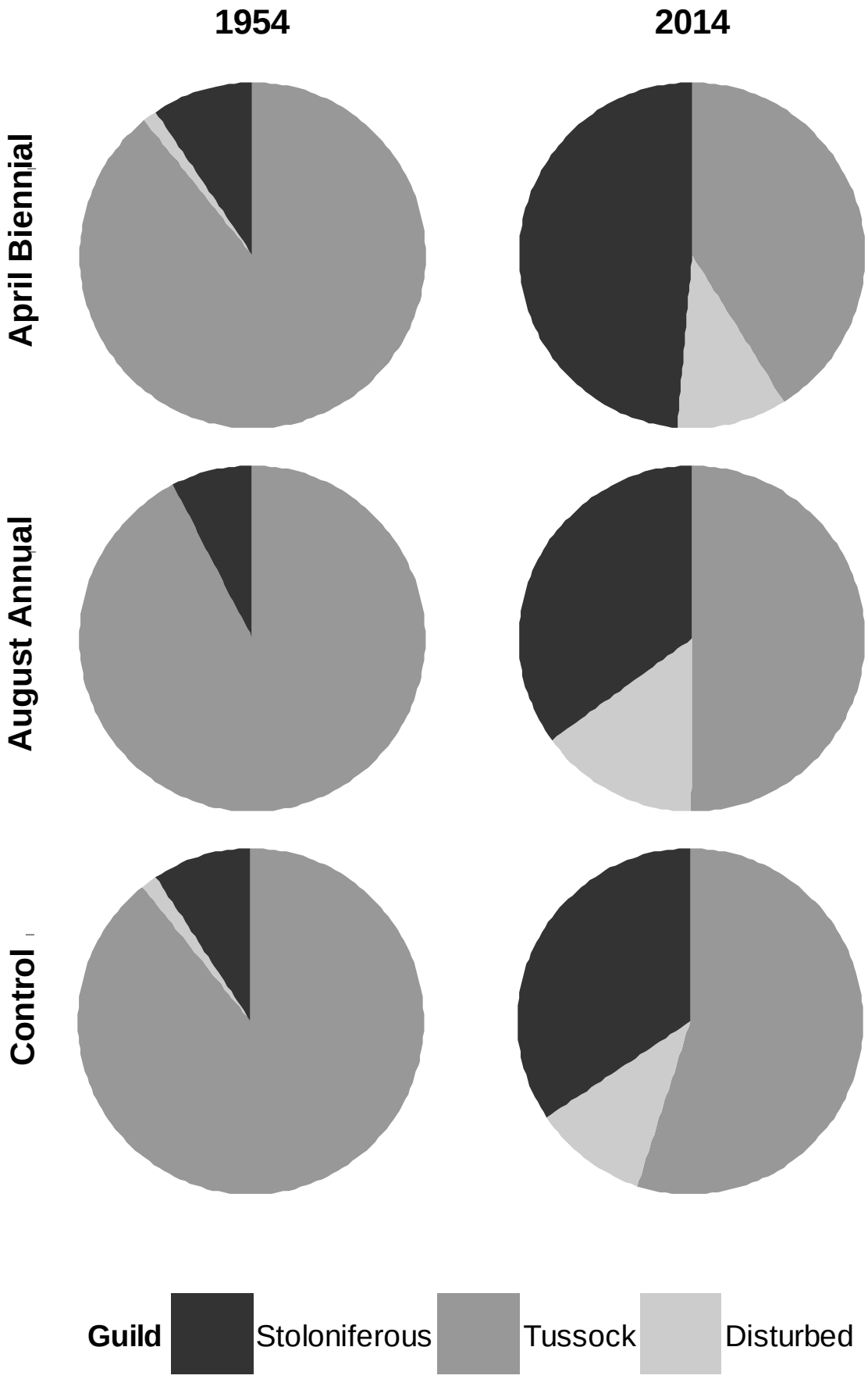

Figure 3.13 Pie charts illustrating percentage composition of functional grass guilds on the April biennial, August annual, and Control treatments in 1954 and 2014 of the EBP's in the Satara region of the Kruger National Park.

3.5. Discussion

My results clearly indicate that there has been a change in grass communities in the EBPs over the last 60 years. Stoloniferous grasses have increased and tussock grasses have decreased, although unexpectedly this change has been larger on the April biennial than on the August annual. Based on the results in Chapter 2 I was expecting the greatest change in the August annual treatment. However, it has been shown that when animals and grazing are excluded, that stoloniferous grasses submit to tall bunch grasses that then become dominant (Stock et al., 2010). The species-level analysis largely conformed to expectations – with some significant exceptions. The tussock grasses (*T. triandra*, *B. radicans*, and *D. eriantha*) all generally declined in abundance on the burn plots and the stoloniferous grasses (*U. mosambicensis* and *P. coloratum*) both increased. These results indicate that biennial, early season fires (with its associated grazing) promote stoloniferous species abundance, whereas the same conditions reduce tussock species. However, as the unpalatable grazing avoider *A. congesta* also increased on the burn plots it is not clear whether the burn treatments resulted in an improved or degraded forage condition for grazing animals.

These results have to be understood with reference to the surrounding landscape. It appears that similar levels of change have occurred in the overall landscape over the same time period (control treatment), which makes it difficult to implicate the fire applications as the cause of these changes. As mentioned above, there are reasons to believe that the analysis of change on the ‘control’ plots is not reliable (in this instance I was comparing species composition of two different sites rather than change over time at one site). Further research would be required to determine the background rates of change in grass communities at the Satara site.

3.5.1. Functional response clusters

Clustering of the grass communities of each EBP treatment (Figures 3.8, 3.9, and 3.10) indicates that some grasses exhibit very similar response to their respective treatments, and show distinct “response clusters”. Although species composition in 2014 (Figure 3.6 B and Figure 3.7 B) was slightly different between the three studied EBP treatments in the Satara landscape, it is clear that, based on their reactions to fire and grazing disturbance, distinct large clusters accompanied by smaller 1 or 2

species clusters have developed in each of the grass communities. The larger clusters were found to be largely composed of species that are most commonly associated with disturbed environments (e.g. *Eragrostis superba*, *Chloris virgata*), but were also well represented by tussock grass species. Although the composition of these larger clusters differed slightly between treatments, they have mostly only seen minor changes since the initiation of the EBPs. Smith et al. (2012) did note a particular lack of change on the Satara EBPs in comparison to the other sites in the KNP. As there were only 2 stoloniferous species (*P. coloratum* and *U. mosambicensis)* found in the study sites, they were always going to represent a small component of these clusters. The fact that grass species of different guilds and ecological status all reacted similarly in these larger clusters, suggests that the ecological status classification system and my functional guild grouping systems are not adequate for determining grass community response at a fine-scale. Nevertheless, the individual reactions of some key grass species showed marked reactions that could illustrate a treatment effect.

3.5.2. Management implications

Bothriochloa radicans has decreased across all three treatments, most extensively on the April biennial treatment. In contrast, Koerner et al. (2014) found that by excluding grazing from the Satara EBPs, *B. radicans* became dominant. This would suggest that grazing helps reduce un-favourable grasses after fires. However, it has been shown that due to the long evolutionary relationship between large herbivores and savanna grasses (Bond et al., 2003), dominance by unpalatable grasses like *B. radicans* is likely to be stimulated in the KNP when palatable species (e.g. *D. eriantha* and *P. coloratum*) are selectively grazed (van Oudtshoorn, 2012; Koerner et al., 2014) and thus prevented from increasing in abundance. Due to the substantial dominance of *B. radicans* throughout the park, coupled with its low palatability and nutrient content, the presence of *B. radicans* in the KNP is of particular concern to park management. The widespread abundance of such an unfavourable grazing species would preferably be replaced by a more favourable species, allowing for improved ecological carrying capacity of the park. *Digitaria eriantha* was largely unchanged on the April biennial treatment, yet decreased on both the control and August annual treatments. *Themeda triandra* increased on the control sites,

decreased on the August annual burns, yet remained unchanged on the April biennial burns. Being considered a “fire-loving” grass, the decrease and lack of change of *T. triandra* on the August annual and April biennial treatments, respectively, is puzzling. However, Robinson et al. (1979) showed that in the False Thornveld of the Eastern Cape of South Africa, *T. triandra* thrives in areas with frequent burning, but under short term heavy utilisation in the post-fire environment, they see only marginal increases. In contrast, *D. eriantha* showed no change under the same conditions (Robinson et al., 1979). This could explain the apparent lack of change observed on the April biennial treatments for both *D. eriantha* and *T. triandra*.

The small yet significant increase in *A. congesta* (disturbed species) on both the April biennial and August annual treatments implies that greater disturbance is taking place on these treatments than on the control treatment, where no change was observed. Although this increase is small in comparison to the remaining key species, it is important to consider this increase in relation to its normal abundance in ecosystems. Disturbed grasses do not normally dominate systems, and therefore such a small increase often reflects a large proportional increase. *Aristida congesta* was actually not observed on the April biennial or August annual treatments in 1954, but are now more abundant than *D. eriantha* and equally as abundant as *T. triandra* (Appendix 2). The two stoloniferous species*, U. mosambicensis* and *P. coloratum* both increased on all treatments. However, *P. coloratum* had a much larger increase on the April biennial treatment, while the largest increase of *U. mosambicensis* was observed on the August annual burn plots. This would suggest that the proliferation of each species either shows a seasonal or fire frequency bias. Regardless, as unpalatable “disturbed” and stoloniferous grasses are associated with grazing lawn communities, their propagation is evidence to suggest that grazing lawn communities could be developing despite the fact that the EBPs still visibly appear to be a bunch grass community. This was also noted by Smith et al. (2012), specifically on the Satara EBPs.

It is my opinion that ecological grass status classes do not adequately represent individual grass ecological functional responses and therefore can be detrimental when making informed conservation/agricultural management decisions. For instance, the contradictory changes observed in *B. radicans* and *P. coloratum*

(Figure 3.12 A), which other than shared Decreaser status are very different grasses, adds support to my views. Regardless, it is evident that the continued and widespread use of this rangeland grass classification method does still provide an adequate general indication of grass community condition. By their definition, my results suggest that the August annual treatments are experiencing the greatest grazing pressure, followed by the April biennial treatment, and finally the control plots exhibiting the least grazing pressure (Figure 3.12B and 3.13). All three treatments showed a decrease in Decreaser species and an increase in Increaser 2 species. This is supported by the results of Danckwerts (1990) who found that Increaser 2 species benefitted from continued grazing by cattle after a burn, and replaced the previously dominant Decreaser species in the Döhne Sourveld of the Eastern Cape (South Africa). Furthermore, it has been shown that Decreaser species are prevented from dominating systems that experience frequent fires by reducing seeding opportunities (Anderson et al., 2012).

Contrary to my results, Smith et al. (2012) suggest that very little change in grass community composition took place on the Satara EBPs (relative to the other treatments in the KNP) over the first 44 years of the experiment. They suggest that the apparent lack they observed was due to greater grazing pressure (Biggs et al., 2003) in relation to the other treatments (despite similar fire intensities etc.). They credit the greater grazing pressure in Satara to the nutrient rich basaltic soil types in the area, as well as greater presence of more palatable grazing lawn grass species (e.g. *U. mosambicensis*). Further, they suggest that, if grazers are more drawn to the frequently burned plots over time, that grass species that would become dominant under such burning conditions would be held back by the increased grazing pressure, resulting in similar grass composition to areas with less frequent burning. This has been observed in the prairie grasslands of North America (Collins et al., 1998; Fuhlendorf & Engle, 2001, 2004). In a study comparing the effects of large herbivore removal on the Satara EBPs to similar sites in North America (Konza), Koerner et al. (2014) found no difference in grass diversity between grazed and un-grazed sites over a 6 year period. Koerner et al. (2014) attributes this to the low response of caespitose grasses to grazing in comparison to North American rhizomatous species. Further, as already stated the long evolutionary relationship between savannas and large herbivores results in a slow turnover of species due to

unpalatable dominant grass species (e.g. *B. radicans*) that increase in abundance when palatable species are selectively grazed (Van Oudtshoorn, 2012; Koerner et al., 2014). Both Smith et al. (2012) and Koerner et al. (2014) agree that the grass communities on the Satara EBPs are resilient to change.

The difference in results from Smith et al. (2012) could potential lie in the 16 year difference between data sets used. Smith et al. (2012) made use of data from 1998/2000, while all my analyses included new data from 2014. Likewise, the contradictory results of Koerner et al. (2014) could be explained by the difference in time periods over which data was collected.

3.5.3. Problems with my research

The nature of the original layout of the experiment makes analysis particularly difficult due to low sample sizes. This was further confounded in my analysis as I decided to ignore the outlier site of Lindanda (deviations in its soil characteristics in comparison to the other three replicates), thus reducing the sample size from four to three. Furthermore, throughout the entire 60 year history of the EBP's, data pertaining to grass composition has only taken place 3 times. This makes it terribly difficult to show a trend of change over time. Additionally, confusion regarding the original methodology appears to have resulted in a few problems. This includes the inability to statistically compare the original data from 1954 to the second data collection bout between 1998 and 2001 (Smith et. al., 2012). Furthermore, data pertaining to forbs was excluded from the original data collection period. Although normally a minor constituent of grazing lawns (McNaughton, 1984), forbs are known to form an important winter period forage source for grazers, and thus may play a role in grazing lawn maintenance during this time. I did not address the forb component of grazing lawns, and as this appears to be an unstudied aspect (Hempson et al., 2014), perhaps this should be included in future work. Hempson et al. (2014) suggest that specific focus should perhaps be placed on the conditions that encourage change in forb community composition in order to improve our understanding of grazing lawns.

3.6. Concluding Remarks

My results suggest that there is a tendency of grass communities on the EBPs to be changing towards a lawn-like community, and perhaps more rapidly so on the April biennial treatment. Stoloniferous and disturbed grass species, which are largely associated with grazing lawns, have increased in abundance while tussocks (bunch grass communities) have decreased. However, this same pattern appears to have been occurring over the entire landscape under normal burning regimes (Control plots). This could be an indicator that there is natural phenomenon occurring, or the natural fire regime in the Satara landscape, causing a general increase in stoloniferous species. One would expect that if grazing lawns had not established themselves after 60 years on the EBPs, it is unlikely to take place. However, the exact conditions as they occurred on my EDS and LDS burns in Chapter 2 are not occurring on the EBPs. It is unlikely, but this could be a result of the slightly larger burns taken place on the EBPs (7ha in contrast to the 5ha in my Chapter 2 experiment). However, it could also be related to the confounding effect that treatment interaction on the EBPs due to their close proximity to each other (Figure 3.3). Nevertheless, the results of my study bring to light the complexity of grazing lawn development - that long-term grazing as a result of burning can result in a shift in grass system state, both composition and structure.

3.7. References

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3.8. Appendices

Appendix 1. All species encountered on the Experimental Burn Plots in the Satara Region of the Kruger National Park, South Africa. The table also shows the guilds that each species was classified into, as well as their ecological status according to Van Oudtshoorn (2012).

Species	Guild	Ecological Status
Aristida congesta	Disturbed	Increaser 2
Bothriochloa radicans	Tussock	Increaser 2
Cenchrus cilaris	Tussock	Decreaser
Chloris virgata	Disturbed	Increaser 2
Digitaria eriantha	Tussock	Decreaser
Enneanpogon cenchroides	Disturbed	Increaser 2
Eragrostis racemosa	Tussock	Increaser 2
Eragrostis trichophora	Disturbed	Increaser 2
Eragrostis superba	Disturbed	Increaser 2
Heteropogon contortus	Disturbed	Increaser 2
Panicum coloratum	Stoloniferous	Decreaser
Panicum maximum	Tussock	Decreaser
Schmidtia pappaphoroides	Tussock	Decreaser
Setaria incrasatta	Tussock	Decreaser
Sorghum versicolor	Disturbed	Increaser 2
Themeda triandra	Tussock	Decreaser
Tragus berteronianus	Disturbed	Increaser 2
Tricholaena monachne	Disturbed	Increaser 2
Urochloa mosambicensis	Stoloniferous	Increaser 2

Appendix 2 The mean difference and change (%) in frequency of grass species found on the three treatments of the EBPs.

Species	April Biennial		August Annual		Control	
	Difference	% Change	Difference	% Change	Difference	% Change
Aristida congesta	7.11	N/A	6.38	N/A	3.29	336%
Bothriochloa radicans	-25.04	-44%	-4.00	-8%	-40.83	-67%
Cenchrus cilaris	-3.12	-97%	0.00	N/A	0.13	31%
Chloris virgata	0.80	N/A	1.86	N/A	0.62	N/A
Digitaria eriantha	-17.92	-100%	-27.95	-99%	-10.73	-58%
Enneanpogon cenchroides	0.27	N/A	0.10	N/A	0.43	N/A
Eragrostis racemosa	0.00	N/A	2.04	N/A	0.28	N/A
Eragrostis superba	0.48	N/A	2.61	N/A	0.02	4%
Eragrostis trichophora	-0.64	-100%	0.00	N/A	0.14	N/A
Heteropogon contortus	0.64	100%	2.61	N/A	4.47	N/A
Panicum coloratum	27.15	302%	4.19	58%	16.72	189%
Panicum maximum	-3.36	-85%	-2.08	-73%	-0.21	-11%
Schmidtia pappaphoroides	0.13	N/A	0.00	N/A	0.00	N/A
Setaria incrasatta	0.09	N/A	0.00	N/A	0.00	N/A
Sorghum versicolor	0.35	N/A	0.00	N/A	0.09	N/A
Themeda triandra	1.06	15%	-10.38	-75%	17.12	223%
Tragus berteronianus	0.00	N/A	1.39	N/A	0.05	N/A
Tricholaena monachne	0.00	N/A	0.00	N/A	0.05	N/A
Urochloa mosambicensis	12.00	2518%	23.21	5851%	8.36	2006%

CHAPTER 4: DISSERTATION CONCLUSION

4.1. Integration of results

As has already been well established (Van de Vijfer et al., 1999; Archibald et al., 2005; Fuhlendorf et al., 2009; Allred et al., 2011), my study shows the important role fire can play in attracting grazers to recently burned areas in a savanna landscape. As predicted, I have identified that grass remains shorter for longer on EDS burns in comparison to LDS burns, even though LDS experience relatively greater grazing visitation (although for a much shorter period). This is attributed to the dry dormant period the EDS burns experience that maintain short grass even in the absence of grazing, and the rejuvenated grazing pressure on these burns after the start of the rains. Regarding the role of fire size, I found that the grazing effect was diluted on the largest fires due to the dispersion of grazers in the burned areas, but grazing was concentrated on the smallest burns, resulting in shorter grass being maintained on the smaller fires. The small size of my burns and the associated increased grazing pressure has shown that fire and grazing together exhibited a greater disturbance than fire alone. Although short grazed patches were maintained for an entire year in EDS burned areas, it is evident that grazing lawns have are unlikely to established themselves over such a short period of time.

My study (Chapter 2) found that grass re-grew to the same heights as under pre-fire conditions within a few months after the rains for both the EDS and LDS burns. However, it is my suspicion that annual burns that experience equal grazing from year to year will result in a subtle decrease in fire intensity as a result of decreased fuel loads. I suspect that this would result in substantially lowered fire intensities in the given area within a few years. Furthermore, if grass is kept shorter for several years, this would also reduce the fires ability to spread within the landscape (Fuhlendorf et al., 2009). The effect that this will have on the fire-grazing interaction and grazing lawn development is yet to be seen, and will only be observed with the continuation of the Fire-Herbivory Program in Satara or other similar research.

I hypothesized that, given sufficient time, the fire-grazing interaction would initiate a change in grass community composition from one dominated by bunch grass

species, into one resembling that of a grazing tolerant system. Although the development of grazing lawns was not expected to take place over a single season (Chapter 2), it is clear that if similar conditions to my landscape experiment are repeated over a 60 year period (Chapter 3, Experimental Burn Plots), that grasses associated with grazing lawns became more dominant (stoloniferous and disturbed grasses), while tufted bunch grasses submit to the conditions of fire and grazing. Contrary to my predictions, grazing tolerant grasses became more dominant in areas burned in the early dry season (April), than in areas burned in the late dry season (August). Although greater grazing intensity was observed on LDS burns after the green flush (Chapter 2), it appears that lower levels of grazing intensity over a longer period of time (more time in a short grass state) caused the greatest shift in grass community composition (EDS Burns).

It is important to note that all the burns in my experiment can be considered small in a practical sense. Very few natural burns will occur at such small scales, and prescribed management burning at this scale is also not common (Archibald et al. 2009; Archibald et al. 2010). My results imply that if land managers are interested in establishing grazing lawn communities either for better grazing or improved biological stability, they could make use of small fires in the early dry season, under heavy grazing, to catalyse grass community change. However, the use of such small fires, specifically in very large areas, may be largely impractical from a management perspective. The main aim of a rangeland or agricultural manager when burning would be to remove moribund material and promote good grazing for animals (Tainton, 1999). This is ideally done at large scales. If land managers were to opt to use smaller fires, they would need to burn multiple small areas, as well as maintain large unburned areas in between them in order for it to be both successful in establishing high quality grazing patches but also successful in establishing enough grazing for the animals on the land. Such a method would require greater resources, infrastructure, and man-power to achieve in comparison to simply applying a single, large-scale burn. Therefore, it is my opinion that a multiple, small-fire approach may only be feasible on small farms or protected areas.

Although the concept of grazing lawns was identified in the 1970's (Lock, 1970; McNaughton, 1984), it is painfully obvious that this biodiversity enhancing phenomenon has not received enough attention in the scientific fraternity. I believe it

is important that research continues on the subject, and specifically the continuation of the fire-herbivory program in the Kruger National Park is imperative to better understanding grazing lawns. Although it has been shown that grazing intensity is greater on the EBP's than in the surrounding landscape (Biggs et. al., 2003), it is my suspicion that grazing intensity is not as high on the EBP's as it was on my landscape experimental burns (Chapter 2). In addition, pertaining to my suspicion that areas burned annually and subject to heavy grazing may become less susceptible to hot (intense) fires and that this may influence grass community change – an important question to ask is if short-grazed areas remain attractive to grazers with time, or do they become less attractive as their productivity decreases? Furthermore, as the EBP's at Satara have exhibited resistance to grass community compositional change over the period of the experiment (Smith et al., 2012; Koerner et al., 2014), I believe it would be useful to investigate the change on the remaining EBP sites in the KNP. This will allow for sampling to take place over a rainfall gradient, as well as the investigation of the role that soil types has in grazing lawn development.

4.2. A way forward

Perhaps the most important aspect of grazing lawn ecology that requires urgent attention is the functional classification of grass species as grazing lawn constituents. It has been reported that environmental factors contribute heavily towards the likelihood of a given grass species possessing the attributes of a grazing lawn grass. That is, a given grass species may possess features of a grazing lawn species (highly palatable, highly grazing resistant), yet due to the environmental conditions it is subject to (as a result of its geographic location), it may not grow in such a way that allows it to develop a carpet like state that is so characteristic of grazing lawns (a characteristic believed to contribute significantly to grazing lawns grazing tolerance). Yet in another geographic location, where environmental factors are more favourable – the same grass species may form a dominant component of a grazing lawn community.

Hempson et al. (2014) describes how grazing lawn communities can be highly complex with multiple functional types of grasses that can constitute its composition, and further describes how distinct types of grazing lawn species can be defined at a

growth-form level. They suggest that the main division in grazing lawn types is a grass species' habit to either spread laterally by means of stolons (above the soil surface) or rhizomes (below the surface), or their habit to persist under heavy grazing in a tufted "dwarf form" (caespitose), that do not spread laterally. Based on hierarchical clustering of "response clusters" to long term fire and grazing, and the reactions key grass species (Chapter 3), it appears that stoloniferous species react similarly, yet tussocks do not. Furthermore, although a general trend is evident, some prominent species of a given ecological grass status group respond as expected, while others do not. This is confirmation that the functional grass guilds I propose are perhaps inadequate for grazing lawn species classification at a species level, and that at a fine-scale, ecological status classification does not paint the full picture. This calls for the absolute necessity for the development of a functional response classification method for grasses to be classified into grazing lawn categories. The classification developed by Hempson et al. (2014) is in my opinion overly-complicated, and will not be useful to the average land manager. I propose that a method similar to that of my functional guilds be developed. This method cannot be species specific, and will require investigation into regional differences in particular species development. I propose that this categorical classification be based on a grass species ability to tolerate heavy grazing, and their palatability. From this, grazing lawn grasses will emerge as a category of grasses that are both palatable and tolerate heavy grazing.

4.3. Final remarks

Fire dependant ecosystems have been classified as endangered at a global scale, particularly savannas and grasslands (Hoekstra et al., 2005). Although the aims of conservation authorities in such systems mostly involve the restoration of ecosystem processes (Hutto, 2008; Sanderson et al., 2008), the role of fire is often overlooked (Bowman et al., 2009). Generally fires are thought of as homogenising elements – and the Satara landscape where I worked is perceived as being overly dominated by fire-prone tall grasslands. The irony of my project is that it was aiming to use a novel fire application to change this: to determine if there is potential for the use of pyric-herbivory to manipulate a grass compositional change, towards that of grazing lawns, and thus increasing biodiversity and ecological integrity of protected areas.

My study suggests that pyric-herbivory may make this possible. The creation of a shifting mosaic of tall grass areas and grazing lawns in savanna systems contribute significantly to system heterogeneity that promotes biological diversity at all trophic levels, and are important for grassland and savanna stability (Tilman & Downing, 1994; Fuhlendorf & Engle, 2001; Pickett et al., 2003; Cromsigt & Olff, 2008). Therefore, the development and maintenance of grazing lawns should be considered a sought after entity in savanna and grassland environments (Novellie & Gaylard, 2013). Although the idea of using fire and grazing to manipulate grazing lawn establishment is a relatively new concept, this study provides insight into the complexity of grazing lawns and their development, highlights the role that fire and grazing play in grazing lawn ecology, and supports the concept that fires and grazing should be viewed as a single disturbance factor; an interaction that should perhaps be considered indispensable for the conservation of fire-driven systems (Archibald et al., 2005; Fuhlendorf et al., 2009).

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